The ecology and behaviour of *Varanus mertensi* (Reptilia: Varanidae)

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Dissertation submitted for the Degree of Doctor of Philosophy
Faculty of Natural Sciences
Edith Cowan University
2006

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Abstract

This study examines numerous aspects of the ecology and behaviour of Merten's Water Monitor, *Varanus mertensi* (Reptilia: Varanidae) including; daily behaviour, diet, foraging behaviour, reproductive seasonality and daily and long-term movements. Findings from over two years of field study of *V. mertensi* found in waterbodies of both the Ord River Irrigation Scheme and surrounding East Kimberley/Victoria River Downs bioregion of Western Australia are presented. This study simultaneously broadens our understanding of the family Varanidae and provides insight into the life of a semi-aquatic faunal species found in waterbodies of the Ord River Irrigation Scheme.

Like other semi-aquatic varanids the daily behaviour of *V. mertensi* incorporates aquatic activity and like other Australian varanids it also varies seasonally. Daily core body temperatures are lower during the dry season when water temperature is low compared to the wet season when water temperature is higher. Seasonal differences in water temperature are also reflected in the daily behaviour of *V. mertensi* that spend more time basking during the dry season. In support of these field observations, laboratory trials showed *V. mertensi* rapidly cool in cold water.

Varanus mertensi is an active wide-ranging opportunistic predator of aquatic and riparian areas with a catholic diet including many relatively small prey items. It moves and searches for prey based on olfactory and visual cues in a similar way to other active foraging varanids. It is equally capable of locating and capturing prey in the terrestrial and aquatic environments and can draw on previous prey capture experience to maximise its foraging efficiency.

Females, like some other tropical Australian varanids lay their eggs during the early dry season. Dry season egg deposition combined with an incubation time of 9-10 months culminates in hatchlings emerging during the following wet season. Female *V. mertensi*, like most varanids, display a synchronous breeding tactic undergoing vitellogenesis just prior to the wet season mating period. However, males are asynchronous undergoing pre-emptive spermatogenesis during the late dry season prior to the mating period.

Adults move between multiple core activity areas within their large long-term activity areas and often do so on a seasonal basis. Daily and long-term activity areas closely resemble the shape of waterbodies in which individuals are found. Some *V. mertensi*, like other Australian varanids, burrow and remain inactive during the late dry season.

This study shows that numerous aspects of the ecology and behaviour of *V. mertensi* are similar to those of other similar-sized varanids just focused around aquatic areas. *Varanus mertensi* occupy a similar ecological niche to other semi-aquatic varanids, that of a wide ranging, active foraging, opportunistic predator of aquatic and riparian areas within their northern Australia distribution.

Declaration

I certify that this dissertation does not, to the best of my knowledge and belief:

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Phillip James Mayes

Acknowledgements

Foremost I would like to acknowledge the Centre for Ecosystem Management and the Strategic Research Initiative Fund of the Faculty of Health, Communications and Science at Edith Cowan University for providing the financial assistance to complete my PhD research. I am grateful to Argyle Diamonds Pty Ltd, The Department of Conservation and Land Management, The Flinders University of South Australia and The University of Western Australia for also providing logistical support. I extend my gratitude to the many volunteers who assisted me with my field studies in the remote Kimberley region of Western Australia. In particular I thank all members of the Saving East Kimberley Endangered Species group for their on-going support throughout my residence in the region.

I acknowledge the academic support and friendship of my supervisors Dr Graham Thompson (Edith Cowan University), Prof Philip Withers (The University of Western Australia) and Emeritus Professor Harry Recher (Edith Cowan University). I thank Dr Tony Start (The Department of Conservation and Land Management), Prof Mike Bull (Flinders University of South Australia) and Prof Donald Bradshaw (The University of Western Australia) for their friendship and academic support throughout my PhD studies. I also thank all research staff and students of both the Centre for Ecosystem Management (Edith Cowan University) and School of Natural Sciences (The University of Western Australia) for their input of ideas on the direction of my research.

Finally I would like to thank all members of my family, my friends and colleagues who kept me sane throughout my enduring PhD. I would like to thank Mrs. Margaret Visciglio for her editorial comments on the final draft of this thesis. I would especially like to thank my life partner Decinta and my parents for their patience, understanding and support during the completion of my PhD.

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General Introduction

1.1 Preamble

This study describes aspects of the ecology and behaviour of the semi-aquatic monitor lizard, *Varanus mertensi* and provides understanding on a semi-aquatic faunal species inhabiting waterbodies of the Ord River Irrigation Scheme (ORIS). It also broadens our understanding of the family Varanidae.

1.2 *Varanus mertensi* (Reptilia: Varanidae)

Varanus mertensi is a medium-sized [adult snout-to-vent length (SVL) > 370 mm] semi-aquatic monitor lizard which inhabits waters of tropical northern Australia from the western side of Cape York Peninsula to north-western Australia (Cogger 1992). Examined in this field study were the daily behaviour, diet and foraging behaviour, reproductive seasonality and spatial movements of *V. mertensi*.

1.3 Aims

The specific aims of this thesis were to describe the following four aspects of the ecology and behaviour of *V. mertensi*:

(1) The daily behaviour;

(2) diet and foraging behaviour;

(3) reproductive seasonality; and

(4) daily and long-term movements

1.4 Organisation of this chapter

This thesis documents the results of two years of field study on *V. mertensi* in the East Kimberley/Victoria River Downs bioregion of the wet-dry tropics of northern Western Australia (Figure 1.1). It reports predominantly on *V. mertensi* inhabiting irrigation waterbodies within the ORIS. Following an outline of the biogeographic characteristics of both the bioregion and ORIS, this chapter outlines the significance of this study of *V. mertensi* in the ORIS. The significance of this study is two-fold, (1) to provide an understanding of the ecology and behaviour of a semi-aquatic faunal species inhabiting waterbodies of the ORIS, thereby filling a significant knowledge gap, and (2) to develop our knowledge of *V. mertensi*, thereby broadening our understanding of the family Varanidae. This chapter outlines the layout of this thesis and provides a guide to subsequent chapters.

1.5 East Kimberley/Victoria River Downs bioregion

The East Kimberley/Victoria River Downs bioregion has a wet-dry tropical climate. Most rainfall occurs between November and March (wet season) with little rain falling between April and November (dry season) (Mc Donald and Mc Alpine 1991) (Figure 1.2). Annual rainfall in the region is variable from 400 mm in the south to 1000 mm in the north (Williams *et al.* 1997). The mean annual rainfall for the township of Kununurra is 790 mm (ABM 2005). Vegetation of the region is low woodland less than 10 m in height with a grassy understory (Beard 1990). Stewart *et al.* (1970) categorized 47% of the East Kimberley/Victoria River Downs bioregion as plains, supporting various perennial grasses on basalt, alluvial and highly productive residual clay soils. Areas in the south are mostly open woodland (Beard 1990).

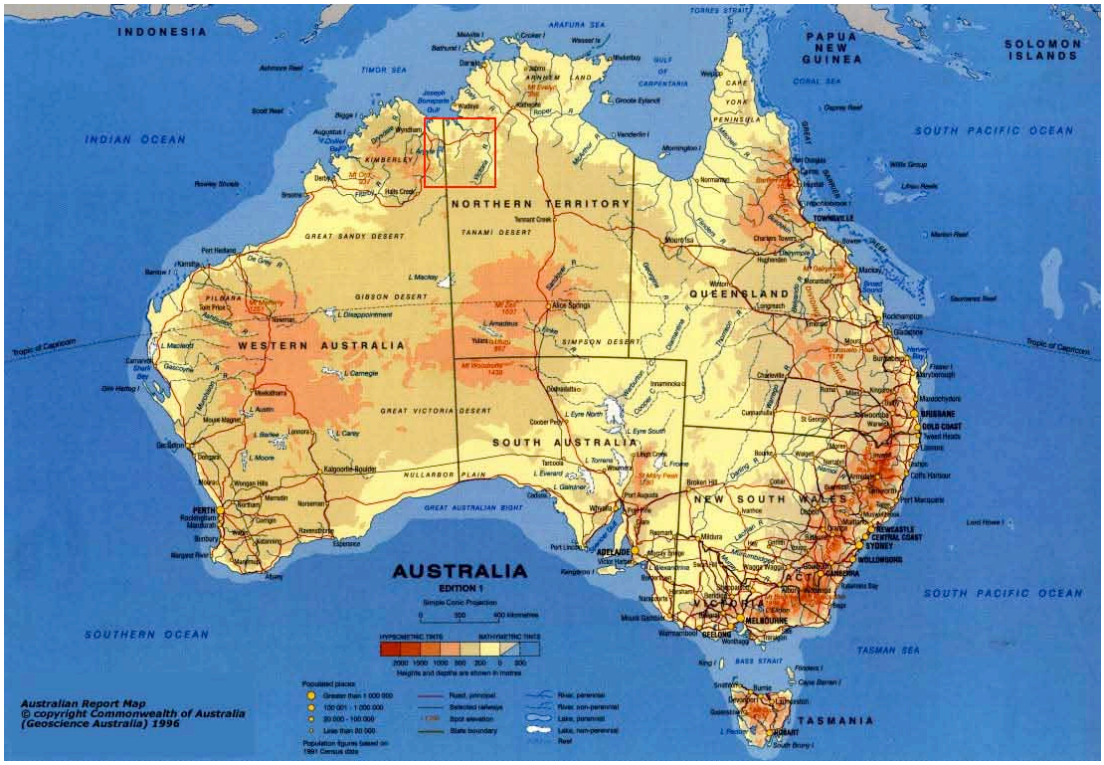


Figure 1.1: Map of Australia showing the location of the East Kimberley/Victoria River Downs bioregion (square outline) (Geoscience 1996).

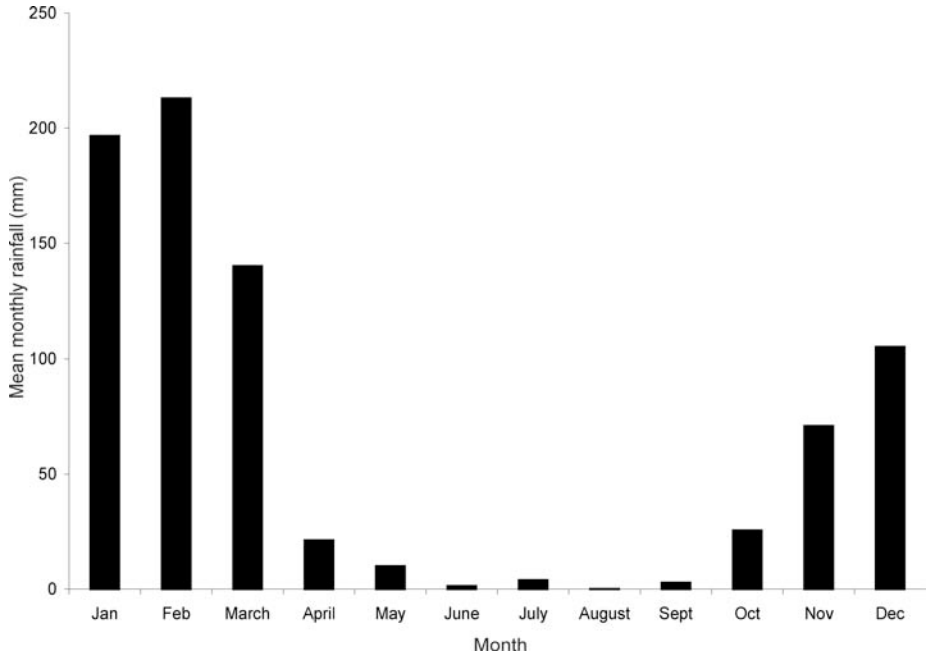


Figure 1.2: Mean monthly rainfall averaged over the years 1962 – 1991 for the township of Kununurra (ABM 2005).

Watercourses flowing through the bioregion are mostly seasonal, flowing only during wet season rains. During the dry season, most watercourses reduce to a

series of discontinuous pools or waterholes (Plate 1.1). Spring-fed watercourses also occur in the region. These may flow year round but can experience similar periods of maximum flow during wet season rains and may also reduce to a series of pools during the dry season (Plate 1.2). I refer to both of these types of watercourses as "natural watercourses" as they have not been modified by the construction of the ORIS. I refer to watercourses modified through construction of the ORIS as "human-altered watercourses". "Natural watercourses" in which *V. mertensi* were examined are briefly described below and their position given in UTM's referenced to the Australian map datum GDS 84.

Thompson's Spring Gorge (UTM: (52) 494477; 8227904): A steep-sided rocky gorge approximately 100 m in depth and 300 m in length. The gorge contains a narrow spring fed watercourse, flowing into two large perennial waterholes of approximately 30 m in diameter and 3-5 m in depth (Plate 1.3).

Four Mile Creek Gorge (UTM: (52) 492163; 8243068): A steep-sided rocky gorge approximately 50 m in depth and 100 m in length. The gorge contains a narrow seasonal watercourse, flowing into numerous seasonal waterholes approximately 5 m in diameter and 1-2 m in depth (Plate 1.4).

Alligator Creek Gorge Waterhole (UTM: (52) 487330; 8227860): A steep-sided rock gorge approximately 30 m in depth. The cutting forms a perennial waterhole approximately 10 m deep and 40 m in diameter (Plate 1.1) on an otherwise seasonal watercourse.

Salerno Gorge and waterhole (UTM: (52) 422722; 8242540): A steep-sided rocky gorge approximately 30 m in depth and 200 m in length. The gorge contains a narrow spring fed watercourse, flowing into several perennial waterholes the largest of which is approximately 60 m x 30 m and 3-5 m in depth (Plate 1.2).

Plate 1.1: Alligator Greek Gorge waterhole during the late dry season of 2002.

Plate 1.2: Salerno Gorge Main Pool during the late dry season of 2002.

Plate 1.3: Thompson's Spring Gorge Waterhole during the late dry of 2002.

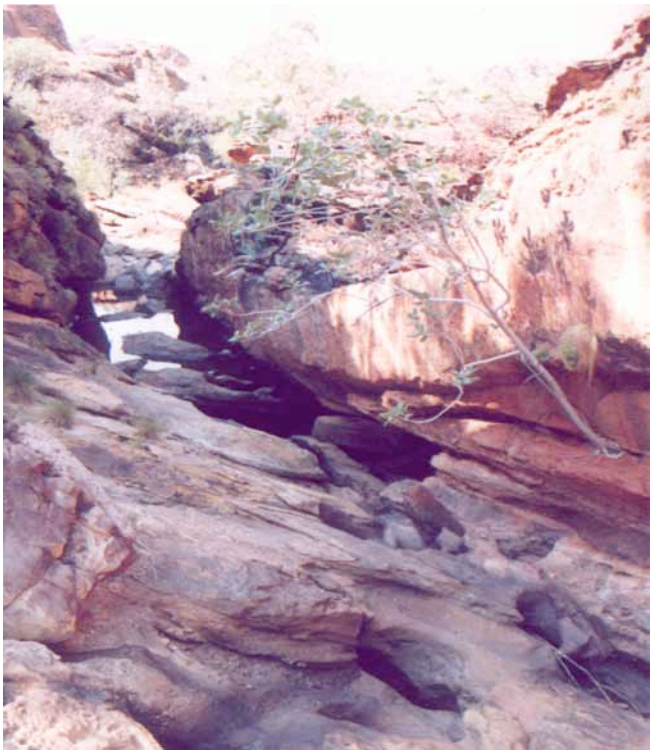


Plate 1.4: Four Mile Creek Gorge during the late dry of 2002.

1.6 Ord River Irrigation Scheme

The ORIS was constructed during the late 1960s to facilitate farming of fertile alluvial soils of the Ord River Valley in the East Kimberley/Victoria River Downs bioregion of tropical Western Australia. The scheme comprises: 1) Lake Argyle formed by the construction of the Lake Argyle Dam approximately 60 km upstream from the townsite of Kununurra (Plate 1.5); 2) Lake Kununurra stretching from Lake Argyle Dam to the Kununurra townsite, length approximately 60 km (Plate 1.6); and 3) a network of water supply and irrigation channels which are fed from Lake Kununurra (Figure 1.3). Each irrigation system supplies water to farms in the following manner. Main supply channels are initially fed water from Lake Kununurra (Plates 1.7 and 1.8) and numerous subsidiary supply channels distribute water further throughout each irrigation area (Plate 1.9). Water is finally fed to farm lots through controlled (gated) irrigation channels (Plate 1.10). Gravity-fed furrows are used to irrigate individual farm lots (Plate 1.11).

Plate 1.5: Foreground; Ord River Lake Argyle Dam wall including hydroelectric outflow. Background; Lake Argyle (DOLA 2000).

Plate 1.6: Foreground; Ord River Diversion dam near the Kununurra townsite. Background; Lake Kununurra stretching approximately 60 km upstream to Lake Argyle Dam Wall (DOLA 2000).

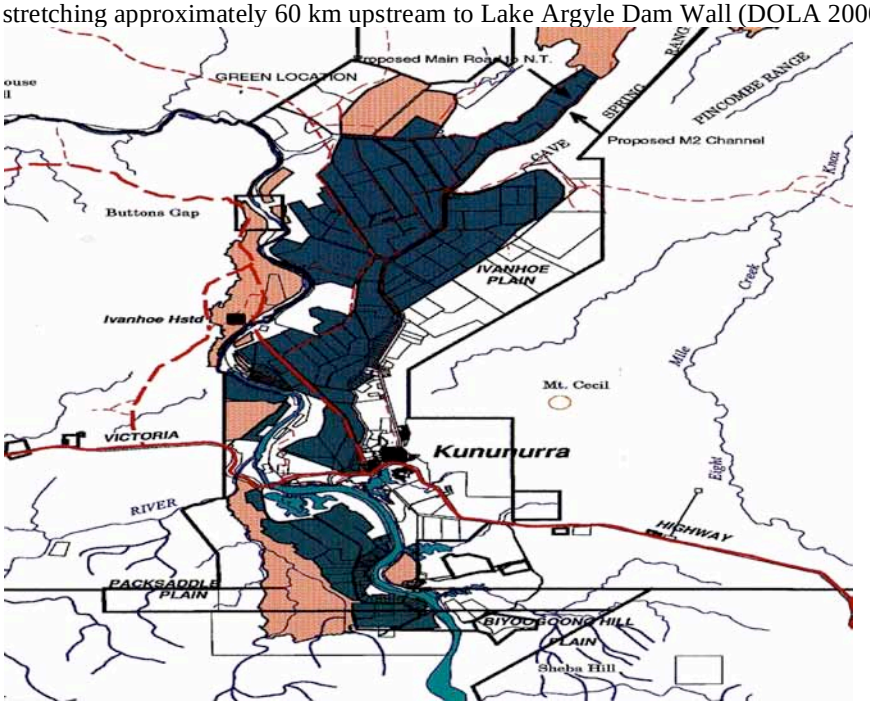


Figure 1.3: Irrigation areas (Ivanhoe Plains and Packsaddle Plains) comprising ORIS (1st stage) on either side of Lake Kununurra. Also shown is the location of the Kununurra townsite (AgWA 2000).

Plate 1.7: Main supply channel (M1) of Ivanhoe Plains Irrigation Area, showing channel access road and riparian vegetation bordering channel.

Plate 1.8: Main supply channel of Packsaddle Plains Irrigation Area, showing channel access road and riparian vegetation bordering channel.

Plate 1.9: Subsidiary supply channel (S2) of the Ivanhoe Plains Irrigation Area showing channel access road and riparian vegetation bordering channel.

Plate 1.10: Controlled/gated farm lot supply channel (center) of the Packsaddle Plains Irrigation Area fed from Packsaddle Main Supply Channel.

Plate 1.11: Controlled/gated farm lot supply channel of Ivanhoe Plains Irrigation Area. Siphons (black poly pipes) gravity feed farms through furrows.

Since construction in the late 1960s, aquatic and riparian ecosystems have established within and along many irrigation watercourses of the ORIS. Before the Lake Argyle and Diversion dams were constructed, the Ord River was a seasonal waterway flowing during periods of high rainfall in the wet season and reducing to sporadic pools during low rainfall in the dry season (Start and Handasyde 2002). Damming of the Ord River has now resulted in a constant water supply throughout the ORIS (Start and Handasyde 2002). An extension of the ORIS, with the planned construction of a second stage (Stage 2, Ivanhoe Plains), is currently being considered. Conflicting water requirements of significant wetlands of the Ord River catchment and the expanding ORIS are currently being debated by scientists, regulatory bodies, environmental managers and the wider community (Doube and Petit 2002). Several wetlands in the Ord River catchment, including Lake Kununurra and Lake Argyle, that support the ORIS are listed under the international 'Ramsar' agreement due to their international conservation significance. These areas are cited for both their abundant endemic flora and fauna, and as refuges for migratory fauna. It would seem appropriate that an understanding of how fauna use the ORIS should be incorporated into future water management plans for the scheme. To provide an understanding of how *V. mertensi* utilises the ORIS is one of the aims of this study.

1.7 The significance of a study of *V. mertensi* in the ORIS

To date few studies have examined faunal species inhabiting the human-altered waterbodies of the ORIS (Doube *et al.* 2004; Kay 2004; Moravec *et al.* 2004) This study contributes to this knowledge short-fall and also provides an opportunity to examine similarities and differences between the semi-aquatic *V. mertensi* and other varanids developing, our understanding of varanid biology.

This study is similar in scope to those of the Bengal Monitor *Varanus bengalensis* (Auffenberg 1994), Grey's Monitor *Varanus olivaceous* (Auffenberg 1988) and the Komodo Monitor *Varanus komodoensis* (Auffenberg 1981). Each of these books documented diet and foraging behaviour, thermoregulatory behaviour and the reproductive cycle of these varanids. This study examines the daily behaviour, diet and foraging behaviour, reproductive seasonality and daily and long-term movements of *V. mertensi* inhabiting predominately the ORIS. It builds on existing ecological, behavioural and physiological knowledge of *V. mertensi* to provide a more complete picture of its ecology and behaviour.

Numerous studies have examined semi-aquatic varanids. These provide substantial knowledge for comparison with the findings of this study of *V. mertensi*. They include the extensively studied *V. salvator* (Abel 1998; Andrews and Gaulke 1990; Andrews 1995; Auffenberg 1979; Auliya and Erdelen 1999; Biswas and Kar 1981; Carl 1993; Daltry 1991; Dryden and Wikramanayake 1991; Dryden *et al.* 1992; Erdelen 1991; Gaulke 1991; Gaulke 1992; Gaulke *et al.* 1999; Gleeson 1981; Khan 1969; Meek 1978; Pandau and Choudbury 1996; Riquier 1998; Shine *et al.* 1996; Shine *et al.* 1998; Sivakumar 2001; Traeholt 1993; Traeholt 1994a, b; Traeholt 1995a, b; Traeholt 1997a,b,c; Whitaker and Whitaker 1980; Wikramanayake and Green 1989; Wikramanayake and Dryden 1993; Wikramanayake 1995; Wikramanayake and Dryden 1999); *V. niloticus* (Angelici and Luiselli 1999; Bayless 1992; Bayless 1992; Branch and Erasmus 1982; Charlton 1973; Cissé 1972; Cloudsley-Thompson 1966; Cloudsley-Thompson 1967; Cloudsley-Thompson 1969; Cowles 1930; De Buffrénil *et al.* 1994; Edroma and Ssali 1983; Hirth and Latif 1979; Kofron 1989; Lonnberg 1903; Modah 1967; Muhigwa 1998; Wood and Johansen 1974; Yeboah 1993); the less studied *V. mitchelli* (Bustard 1970; Shine 1986; James *et al.* 1992; Losos and Greene 1988); *V. indicus* (Bustard 1970; Dryden 1965; Kukol 1993; Irwin *et al.* 1996; Losos and Greene 1988; Mccoid and Hensley 1991; McCoid

and Witteman 1993; Nelling 1995; Philipp 1999; Uchida 1966; Wikramanayake and Dryden 1988) and *V. semiremex* (Dunson 1974; Horn 1985; James *et al.* 1992; Losos and Greene 1988; Mertens 1959; Peters 1969).

Also providing knowledge for comparison with the findings of this study are numerous studies of Australian varanids. These include *V. tristis* (Bartholomew and Tucker 1964; Thompson and Pianka 1999; Thompson *et al.* 1999), *V. gouldii* (Bennett 1972; Bennett 1973; Bradshaw and Rice 1981; Bradshaw *et al.* 1982; Christian 1995; Christian *et al.* 1995; Christian and Weavers 1996; Johnson 1976; Koch 1970; Pianka 1982; Rice 1982; Shine 1986; Tenhu *et al.* 1999; Thompson 1992; Thompson 1994; Thompson 1995; Thompson 1996; Thompson 1996a,b; Thompson and Withers 1992; Thompson *et al.* 1992; Thompson and Withers 1997), *V. rosenbergi* (Green 1969; Green 1972; Green and King 1978; King 1977), *V. glebopalma* and *V. glauerti* (Sweet 1999), *V. panoptes* (Blamires 1999; Bennett 1992; Christian *et al.* 1995; Christian *et al.* 1996; Christian and Weavers 1996; Christian 1995; Shine 1986; Thompson and Withers 1992; Valentic 1994), *V. varius*; (Carter 1991; Carter 1999; Weavers 1989; Weavers 1993), *V. caudolinateus* (Thompson *et al.* 1992; Thompson 1993; Thompson and King 1995), *V. giganteus* (King *et al.* 1983; King *et al.* 1989; Green *et al.* 1984; King and Green 1993; Horn and Visser 1988; Irwin 1996; Pianka 1982; Pianka 1994; Stirling 1912; Thompson *et al.* 1995), *V. gillenii* (Bickler and Anderson 1986; Carpenter *et al.* 1976; Christian *et al.* 1996; Gow 1982; Husband and Vincent 1999; Murphy and Mitchell 1974; Peters 1970; Pianka 1969; Thompson and Withers 1997), *V. scalaris* (Christian and Bedford 1995; Christian *et al.* 1996; Masini 1988) and *V. spenceri* (Christian *et al.* 1996; Christian 1979; Pengilley 1981; Valentic and Turner 1997).

1.8 Knowledge of *V. mertensi*

This study expands and compliments previous studies of *V. mertensi* to form a more complete picture of the species. By comparing *V. mertensi* with other varanids, this study also builds on our understanding of the family Varanidae. Previous studies of *V. mertensi* have presented data on diet and reproductive cycle (Shine 1986), thermoregulation (Christian and Weavers 1996), energetics and water flux (Christian *et al.* 1996), gas exchange and ventilation (Thompson and Withers 1997), standard evaporative water loss and metabolism of juveniles (Thompson and Withers 1998) and solar absorbance (Christian *et al.* 1996). Observations of *V.*

mertensi feeding (Hermes 1981) and mating in the field (Blamires 1996) have also been reported. Reports of egg incubation times (Eidenmuller and Wicker 1995), husbandry techniques (Irwin 1986) and combat behaviour (Horn *et al.* 1994; Murphy and Lamoreaux 1978) have also been reported for captive *V. mertensi*.

1.9 Thesis outline

This thesis comprises seven chapters; a general introduction, general methods, four data chapters, and a concluding synthesis chapter. Each data chapter considers an aspect of the ecology and behaviour of *V. mertensi*. First documenting daily behaviour allows diet and foraging behaviour to be interpreted in the context of an individual's temperature requirements. Likewise, considering diet and foraging behaviour before examining the reproductive cycle of *V. mertensi* allows seasonal prey availability and its effects on reproductive effort to be considered. Finally, a daily and long-term movement's chapter draws on findings of previous data chapters for interpretation.

The thesis concludes with a general discussion integrating the findings of these four data chapters. The general discussion formulates a picture of the ecology and behaviour of *V. mertensi* compared to other varanids, providing new insight into the family Varanidae. It also outlines the life of *V. mertensi* in waterbodies of the ORIS providing new insight on the use of these areas by a semi-aquatic faunal species.

-Chapter 2-

General methods

2.1 Introduction

This study incorporated both field and laboratory components. The field component of this study was completed over two years between January 2001 and February 2003 in the East Kimberley/Victoria River Downs bioregion of Western Australia. Laboratory experiments and analysis of field samples were completed between February 2003 and June 2005. To avoid repetition, methods common to multiple chapters are outlined in the following sections.

2.2 Materials and methods

For the field component of this study, 40 thermo-sensitive radio-transmitters were implanted into adult *V. mertensi* in the East Kimberley. Radio-tagged individuals were frequently located during 2001, 2002 and early 2003. Movements of these animals were examined to understand the long-term movements of *V. mertensi*. The core body temperatures (T_b) and behaviour of these individuals were also examined for seasonal differences. Numerous radio-tagged individuals were also continuously observed during their active day to provide a link between daily behaviour, diet, foraging behaviour and movement data.

Techniques used to capture individuals, implant radio-transmitters and radio-track individuals are described in the following sections.

2.2.1 Animal capture, handling and release

Varanus mertensi were captured using numerous techniques including; capture by hand, noosing and trapping. Hand capture in the water involved a researcher grabbing an individual while it lay still on the benthos. Individuals captured were grasped by the tail and additionally restrained by grasping behind the neck in both the water and on land.

To approach wary individuals for hand capture on land, a rod and noose was often employed, this proved highly successful. The noose rod used was a 4 m long sturdy fishing rod with a noose of strong non-stretch nylon cord. To noose an

individual two people were often required. While one person attracted the attention of the monitor by waving their hands the other slipped the noose over the head of the distracted individual from behind.

Baited treadle traps were also used to trap *V. mertensi*. Traps were modified "tomahawk" traps that were approximately 1200 mm x 300 mm x 300 mm with a grid mesh of 20 mm². Traps were baited with tinned sardines, kangaroo meat, lamb heart or ox heart, or a combination of some or all. Baited traps were set on the water line with the treadle mechanism just out of the water. Traps were visited and re-baited every 24 hrs.

All captured animals were transported in calico bags in an air-conditioned vehicle (≈ 24 ° C) and held in air-conditioned premises before surgery, blood sampling or stomach flushing. Animals recovering after invasive procedures were also kept in air-conditioning. Animals soon to be released were given approximately 60 minutes to equilibrate to ambient conditions after being held in an air-conditioned environment.

All animals were released at their site of capture during their usual activity period. Where possible, release took place during the mid-to-late morning giving a recovering individual enough daylight hours to reorientate itself and find a suitable overnight refuge before nightfall.

2.2.2 Measurements

All *V. mertensi* were weighed using a calibrated spring balance. Snout-to-vent length (SVL) and tail length (TL) were measured using a tape measure. The sex of *V. mertensi* was firstly assessed by attempting to evert the hemipenis of males in the field. In many instances suspected males failed to evert a hemipenis as extensive tail musculature prevented sufficient pressure being applied to the post-cloacal ventral surface. The definitive sex of individuals was determined using a combination of both hemipenile eversion and hormonal analysis of blood samples taken from captured animals (Chapter 5).

2.2.3 Surgical implantation of internal thermo-sensitive radio transmitters

Individuals were anaesthetised using inhaled Isoflurane ether. A restrained animal's head was placed in a sealed plastic bag containing several cotton balls soaked in approximately 5 ml of isoflurane. The amount of isoflurane required varied

with the size of the animal. To account for this excess anaesthetic was used and the remaining amount reused. The anaesthetic took approximately 5 to 15 minutes to take effect, but this varied up to 20 minutes in instances where individuals initially held their breath.

Animals were deemed fully anaesthetised when pulmonary activity ceased and eye lids remained closed. A pinch test was applied to the tail of animals to assess loss of touch sensation before continuing with surgical procedures.

An area approximately 10 x 10 cm on the lateral side of the abdomen, 2-3 cm forward of the hind limbs was cleaned with 70% Chlorhexidine solution. All surgical instruments and the operating area were also sterilised with Chlorhexidine, as were radio-transmitters. A small incision, 2-3 cm, was made longitudinally in the area treated with Chlorhexidine using surgical scissors. After separation of the skin and intact muscle layers with forceps, access was gained to the abdominal cavity. Transmitters (Holohil Systems Ltd, Model 2I-T) weighing 3 g (2.5 cm x 0.6 cm) with an external whip antennae of length approximately 10 cm were inserted into the abdomen. Transmitters were positioned longitudinally within the abdominal cavity. A flexible brass tube of diameter 1 mm and length 20 cm was threaded between the skin and muscle layers from the anterior point of incision along the lateral fold of the animal to just behind the head. The external antenna was positioned in the tube and the tube removed through a small incision made just behind the head, leaving the antenna in place under the skin along the lateral fold. This technique ensured the antennae was straight and provided maximum signal strength and hence detection range.

The small incision behind the head, made for the extraction of the brass antennae leader, was sealed using Vetbond (superglue). The larger incision in the ventral surface was closed with dissolvable sutures. Suturing began 1-2 mm behind the cut surface of the skin and the two surfaces were held neatly together while sutured. Sutures were covered with Vetbond to assist in adhesion and to prevent sutures being exposed to the environment for several days until the glue abraded away.

Animals were revived from anaesthetic by inserting a small flexible plastic tube (surgical-grade Silastic) of diameter 2 mm; through the glottis to a depth of approximately 5 cm. Animals were artificially aspirated, via this tube, until most of the Isoflurane within the lungs was removed. Usually between 2 and 3 breaths into

the lungs was sufficient for this task. Following removal of Isoflurane, animals usually showed signs of increased heart rate within minutes. Most animals had full pulmonary function in 5-10 minutes. Recovering animals were assessed continually for both increased cardiac and pulmonary activity. In some instances animals did not immediately restore strong cardiac activity. On these occasions gentle cardiac massage was employed until strong cardiac activity was noted. Upon establishing strong cardiac activity, pulmonary activity normally followed. After cardiac and pulmonary functions were re-established individuals usually awoke within 10-15 minutes. Recovering individuals were held overnight to fully recover before being released at their point of capture the following day. Surgical implantation of radio-transmitters using this technique revealed minimal long-term effects on individuals over the two year study period.

Before release each animal was allocated a unique capture number for future identification. Numbering involved a toe clipping system that removed no more than one toe from any one foot while the animal was anaesthetised.

2.2.4 Calibration and re-calibration of thermo-sensitive radio-transmitters

Radio-transmitters were temperature-sensitive enabling measurement of core body temperature (T_b). Transmitters increased their pulse rate with temperature in a curvilinear relationship. Calibration involved measuring the time taken for 21 pulses to emit from active transmitters over a range of temperatures. This number of pulses was used throughout laboratory and field work as it adequately estimated pulse rate and allowed for a quick calculation of pulse interval in a field situation. Pulse interval was taken as the recoded time for 21 pulses to emit divided by 20 and expressed in milliseconds. Laboratory calibration measurements were made with transmitters in a controlled temperature water bath at 20, 25, 30, 35, 40, 45 and 50 ^{o}C. Transmitters were left in the water bath until their pulse rate was constant, indicating that the temperature of the transmitter had equilibrated with the water bath. A quadratic regression equation was used to describe the relationship between transmitter temperature and pulse interval for each of the 40 radio-transmitters.

At the completion of the study, a total of nine of the 40 radio transmitters were recovered. Four of these nine transmitters were re-calibrated using the procedure outlined above. The recalibration of all 4 transmitters revealed no detectable shift in the thermal sensitivity of any of the transmitters (Figures 2.1).

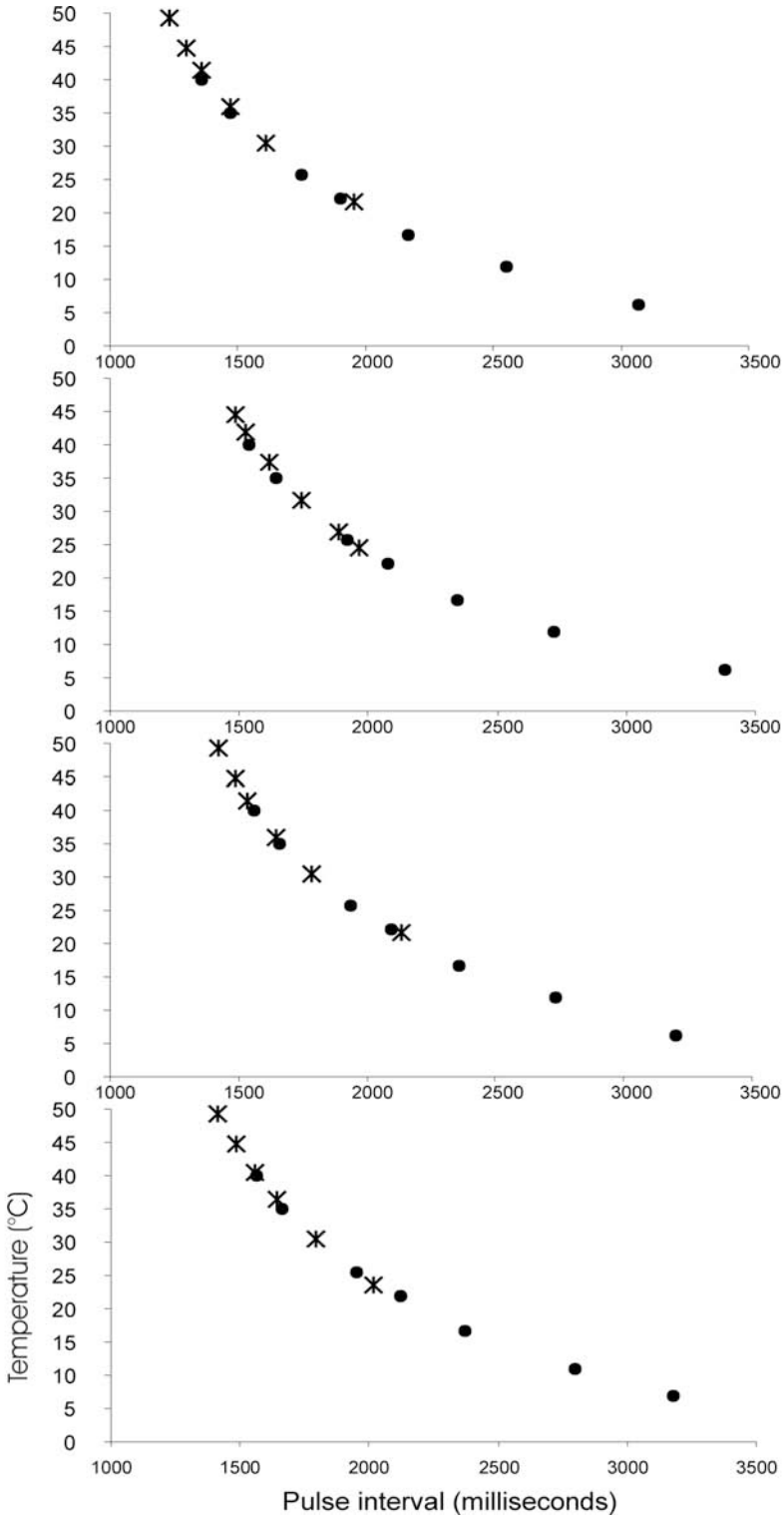


Figure 2.1: Pulse interval at different temperatures for recovered radio transmitters; 61098, 61099, 61115 and 61102 (Holohil Systems Ltd). * indicates initial calibration before implantation in 2000. ● indicates re-calibration after recovery in 2003.

2.2.5 Tracking of radio-tagged *V. mertensi*

An omni-directional antenna (Titley Electronics Pty Ltd) connected to a 150 MHz radio receiver (Bio-telemetry Pty Ltd) was used to initially locate radio-tagged

V. mertensi. This antenna was mounted approximately 2 m above ground, on top of a vehicle, to maximise the detection distance of radio signals. As individuals were often found along linear watercourses, driving adjacent to these watercourses was an effective way to detect the general location of an individual. Where vehicle access was restricted the omni-directional antenna was mounted onto a 4WD all-terrain motorbike at a height of 1-2 m.

After a signal was detected using the omni-directional antenna, a directional Yagi (3 element) antenna (Titley Electronics Pty Ltd) was used to determine the exact position of radio-tagged individuals. When an exact position could not be determined an individual's position was estimated using a triangulation technique. This involved taking three positional fixes to triangulate the approximate position of an individual. This proved a useful technique for approximating the position of an individual in a swamp, large water body or on the opposite side of an irrigation channel.

2.2.6 Data recorded for radio-located *V. mertensi*

Throughout the field study, the position of individuals was recorded using a GPS Receiver Unit (Garmin GPS 2 Plus). Individuals were also observed, from a distance so as not to perturb an animal's behaviour, upon location and their behaviour was categorised as:

Not seen: An individual was not be seen when located or was thought to be inactive, as indicated by a stationary radio signal, but not thought to be located in a burrow.

Burrow: An individual was located with its radio signal emitting from a burrow.

Active but not seen: An individual was located but not seen and thought to be active as indicated by a moving radio signal.

Swimming: An individual was located moving in the water.

Basking: An individual was located stationary lying on a substrate in direct sunlight.

Walking: An individual was located moving in the terrestrial environment.

Simultaneously both the temperature of a thermocouple placed in direct sunlight and in the shade 1 m above the soil substrate and away from other radiant heat sources was measured. The temperature of the thermocouple submerged at a depth of 1 m in water and in soil substrate at a depth of 15 cm closest to the active individual was also measured. The thermocouple was allowed to acclimate and

stabilise between each temperature measurement. The pulse interval of the radio-transmitter and hence T_b of individuals was calculated by measuring the time taken for 21 pulses to elapse as described above.

2.2.7 Continuous observation days

Radio-tagged individuals were often continuously observed throughout an active day to document their daily behaviour, T_b and movements. Where possible animals were observed every ten minutes from when they first emerged to when they retreated into their overnight refuge burrows. Crude measurements of ground surface temperature in direct sunlight and in full shade, below ground temperature and temperature in the water were simultaneously recorded every 10 minutes using temperature probes and loggers. Two temperature probes and two temperature data loggers (Hobo Tinytag Ultra temperature sensitive data-loggers Hasting Data Loggers Pty Ltd) recorded simultaneously the temperature of a logger unit placed on the ground in direct sunlight, a probe submerged in water at a depth of 1 m, a logger placed on the ground in full shade and a probe embedded in the ground at a depth of 15 cm. It is appreciated temperature throughout the water column is variant however water temperature was taken at a standard depth of 1 m as this reflects the area of the water column most utilised by aquatically active *V. mertensi* (Pers. Obs). Similarly soil temperature was measured at a standard depth of 15 cm to crudely reflect underground soil temperatures that may be experienced by a burrowed individual. Owing to manufactures specifications, the maximum temperature recorded by either a logger or a probe was 51.9 °C.

Several authors have reviewed the use of physiological models in the study of heating and cooling rates of reptiles (Dzialowski and O'Conner 1999; 2001). Deploying physiological models representative of study species has been used to give an indication of the maximal operative temperatures obtainable by reptiles studied in field situations including varanids (Christian and Weavers 1996). In addition to measuring the environmental temperatures outlined above, the water temperature inside a representative "model" adult *V. mertensi* was recorded simultaneously every 10 minutes. It was envisaged this would give an indication of maximal operative temperatures obtainable by field active individuals if they remained in direct sunlight throughout their entire active day. The water temperature of the water-filled model was recorded while the model was in full sunlight using a

thermocouple attached to a digital voltmeter. The dimensions of the copper tubing model were 400 mm x 60 mm (diameter). It was envisaged that these dimensions would reflect the body dimensions of an adult *V. mertensi* with a SVL of 400 mm. The copper tubing model was painted and covered with a preserved skin from a dead adult *V. mertensi* to replicate the solar absorbance of an adult *V. mertensi*. The model was filled with water to simulate the thermal inertia of *V. mertensi*. It is appreciated that a copper tube filled with water and placed in full sunlight has different thermal properties to that of an animal lying in the sun. However, the primary purpose of the model was to demonstrate that the T_b of a *V. mertensi* remaining in the sun would rise to above its critical thermal maximum temperature. This would indicate that to survive, an individual would need to down-regulate its temperature by physiological or behavioural means.

Behavioural observations were also categorised and recorded for every 10 minute period. This coincided with measurements of core body temperature, environment temperatures and model temperature. Behavioural observations were divided into the behavioural categories outlined in the above sections (data recorded from regularly radio-relocated animals).

Finally the position of observed individuals were also recorded every 10 minutes. Coordinates were obtained after an individual had moved from a location allowing the observer to obtain a GPS fix without disturbing an active individual.

-Chapter 3-

Daily behaviour of *V. mertensi*

3.1 Summary

Both laboratory and field data show that activity in water cooler than core body temperature (T_b) quickly reduces the T_b of *V. mertensi*. Under laboratory conditions time taken to both heat and cool increased with body mass and heating and cooling times were 6-7 times faster in water than in air. In the field, different-sized *V. mertensi* basking in direct sunlight under different ambient conditions heated at rates between 0.02 - 0.11 °C min^{-1}. Different-sized *V. mertensi* observed in the field entering water of different temperatures cooled at rates between 0.05 – 0.19 °C min^{-1}.

Varanus mertensi emerged from overnight refuge burrows at 08:00 hrs (WST) during both wet and dry seasons and retreated during the dry season at 16:30 hrs and 15:30 hrs (WST) during the wet season. There was variation in the daily T_bs and behaviour of individuals observed on different days. One individual observed for multiple days in both seasons showed seasonal differences in its mean daily T_b profile and behaviour. A “typical” active day for a *V. mertensi* showed fluctuations in T_b throughout the day during both seasons. Fluctuations were more numerous during a dry season day than during a wet season day and coincided with alternating periods of basking and swimming. Individuals displayed different behaviour during the two seasons, with extensive aquatic activity and minimal basking throughout the day during the wet season and less aquatic activity supplemented with extensive basking periods during the dry season. Data combined from all observation days for active *V. mertensi* also showed seasonal differences in T_b and behaviour. A higher proportion of most hours throughout a day were spent basking during the dry season whereas a higher proportion were spent swimming during the wet season.

Despite seasonal differences in their active day T_bs, general T_b profiles of observed individuals were similar to those of other heliothermic varanids. A day for *V. mertensi* began with a morning period of increasing core body temperature,

followed by relatively constant temperature throughout the middle of the day, before a reduction in temperature prior to retreat. The mean T_bs maintained by active *V. mertensi* of 27 – 33 °C during the dry season and 32 – 34 °C during the wet season were lower than those reported for other terrestrial varanids. Interestingly, mean daily T_bs of *V. mertensi* observed in this study only reached 33 °C, which is below the minimum experimental preferred temperature of *V. mertensi* of 33.1 °C during the dry season. The mean midday T_b (11:00 – 16:00 hrs) of active *V. mertensi* during wet season months of 33.5°C was significantly higher than during the dry season of 31.3 °C. These data contrast with a previous study of *V. mertensi* in the Northern Territory and suggests *V. mertensi* are much like other Australian varanids that also show seasonal differences in active T_bs.

3.2 Introduction

To understand the ecology and behaviour of an ectothermic reptile it is important to first understand its thermal requirements as these requirements are likely to play an important role in shaping its daily behaviour. Understanding behaviour used to meet these thermal requirements is paramount to interpreting limitations imposed by a reptiles thermoregulatory needs to function physiologically. The overall aim of this study is to develop an understanding of the ecology and behaviour of *V. mertensi*, inhabiting waterbodies of the ORIS and East Kimberley. An appreciation of the behavioural strategies used by *V. mertensi* to meet its thermal requirements in these areas is therefore important.

3.2.1 Reptilian thermoregulation

The physiological and behavioural means by which ectothermic reptiles regulate their body temperature has been examined by numerous authors using a wide variety of techniques (Avery 1979; Bakken 1976; Bartholomew and Tucker 1964; Boland and Bell 1979; Clark *et al.* 2005; Dzialowski and O'Conner 1999; 2001; Grigg *et al*. 1979; Fraser 1985; Hertz *et al.* 1993; Huey 1974; Johnson and Voigt 1978; Seebacher 2000; Seebacher and Grigg 2001; Seebaker and Franklin 2003; 2005; Seebacher and Shine 2004 and Wood *et al.* 1981). Despite great advancement in this area of research several authors have highlighted problems in drawing comparisons between the results of different studies utilising different methodologies (Seebacher and Shine 2004 and Grigg *et al* 1979). In their review

papers (Seebacher and Shine 2004 and Grigg *et al* 1979) examined the use of different techniques in the study of reptile temperature regulation and physiology providing common methodologies that can be used across studies of different reptiles. The expression of the heating and cooling rates of reptiles, which facilitates meaningful comparison between different studies, has also been examined by several authors (Bakken 1976; Boland and Bell 1980; Dzialowski and O'Conner 2001; Fraser 1985). For example expressing changes in body temperature in °Cmin^{-1} limits comparison between different studies where animals experience different changes in temperature. An alternative method which gives an indication of heating and cooling rates utilises thermal time constants and provides for comparison between studies where animals experience different changes in temperature (Bakken 1976; Boland and Bell 1980; Dzialowski and O'Conner 2001; Fraser 1985; Grigg *et al.* 1979 and Seebacher and Shine 2004). A good understanding of the heating and cooling rates of reptiles is required to interpret behavioural observations made in the field and draw conclusions on the thermoregulatory ability of different reptile species. To provide data on the experimental heating and cooling rates of *V. mertensi* which is directly comparable with that of other reptiles is one objective of this chapter.

Most varanids regulate their T_b in a similar way to many ectothermic reptiles by modifying their behaviour to maintain T_bs within a narrow range while active (Christian and Bedford 1995; Christian and Weavers 1996; King 1980; Meek 1978; Stebbins and Barwick 1968; Thompson *et al.* 1999; Traeholt 1995; Tsellarius 1997; Wikramanayake and Green 1989; Wikramanayake and Dryden 1993). Varanids have also been shown to be capable of physiologically regulating their T_b through altering heart rate (Clark *et al.* 2005; Seebacher 2000; Seebacher and Grigg 2001) and blood flow (Seebacher 2000). The daily T_b profile of most varanids is characterised by a morning period of steady temperature gain following emergence, a midday period of relatively constant T_b within a narrow temperature range, and a slow decline in T_b towards the late afternoon before retreat (Christian and Weavers 1996; Christian and Bedford. 1996; Meek 1978, Seebacher and Grigg 2001; Thompson *et al.* 1999; Traeholt 1995). Like other reptiles, varanids also have a minimum temperature (CT_{min}) below which they do not function well physiologically (Bartholomew and Tucker 1964; McNab 2002). The T_bs of terrestrial varanids are generally higher than those of other reptiles (Bartholomew and Tucker 1964; McNab 2002). For example, *V. gouldii* maintains T_bs around 35 -38 ˚C (King 1980; Pianka 1994), *V. eremius*

around 37.3 ˚C (Pianka 1994), *V. caudolineatus* about 37.8 ˚C (Pianka 1994), *V. komodoensis* around 34.5 ˚C (Wikramanayake et al.. 1999), *V. giganteus* around 36 ˚C (King *et al.* 1989) *V. scalaris* around 35.6 ˚C – 39 ˚C (Christian and Bedford 1996), *V. griseus* around 33.1 ˚C - 34.5 ˚C (Ibrahim 2000), *V. panoptes* around 35.8 ˚C - 37.6 ˚C (Christian and Weavers 1996) and *V. rosenbergi* around 34.0 ˚C - 36.5 ˚C (Christian and Weavers 1996). Both Pianka (1994) and Thompson *et al.* (1999) reported lower T_bs for *V. tristis* of 33.2 ˚C and 34.8 ˚C respectively. Both authors suggested that the lower T_bs of *V. tristis* may reflect their predominately arboreal lifestyle in cooler microhabitats. Semi-aquatic varanids have also been reported to have lower T_bs than terrestrial varanids. For example, *V. mertensi* have T_bs of 33.1-35.5 ˚C (Christian and Weavers 1996); *V. salvator* of 29.5 – 37 °C with a mean daily T_b of 30.4 °C (Traeholt 1995) and 27 – 32 °C (Wikramanayake and Green 1989). It has been suggested that, much like the arboreal *V. tristis*, the lower T_bs of semi-aquatic varanids may reflect their lifestyle in cooler (aquatic) microhabitats (Christian and Weavers 1996; Traeholt 1995; Wikramanayake and Green 1989). Like all reptiles, varanids also have a critical thermal maximum temperature (CT_{max}) above which they die. This temperature has been shown to be as high as 50 ˚C for several species (Auffenberg 1981; Curry-Lindahl 1979; Lutterschmidt and Hutchison 1997; Pianka 1986; Pianka *et al.* 2004).

As for other reptiles the thermal inertia of varanids increases with increasing body mass, meaning that large varanids heat and cool slower than smaller conspecifics (Bartholomew and Tucker 1964; Bradstromm 1973; Earll 1982; Green *et al.* 1991; King 1991; King *et al.*. 1989; McNab and Auffenberg 1976; Seebacher 2000; Seebacher and Grigg 2001). It has been suggested that large body size allows larger varanids to sustain their T_bs with less behavioural modification of body temperature than smaller conspecifics (Green *et al.* 1991; King *et al.* 1983; King *et al.* 1989; Heger 2000; McNab and Auffenberg 1976; Seebacher and Grigg 2001; Seebacher 2000; Wikramanayake *et al.* 1999). Conversely, small varanids (or juveniles of larger species) are more dependent on behavioural modification of T_b to sustain their temperatures (Heger 2000; Wikramanayake *et al.* 1999). Interspecific variation in solar heat absorbance by varanid species has also been reported (Christian *et al.* 1996). Unlike some other families of reptiles, no varanid species has been shown to vary its solar absorbance for the purposes of thermoregulation (Christian *et al.* 1996). Interestingly, the solar absorbance of *V. mertensi* of 89.0% at

15 ˚C and 89.4% at 35 ˚C is amongst the highest for an Australian varanid species (Christian *et al.* 1996). They suggested that this high absorbance (reflecting the dark dorsal skin colour of *V. mertensi*) may facilitate rapid heating when basking after emergence from the water. Christian and Weavers (1996) found that the mean midday field active T_b of *V. mertensi* did not differ significantly between the wet and dry seasons, unlike seasonal differences identified for other Australian varanids. Given their lower T_b and lack of seasonal differences in field T_bs, Christian and Weavers (1996) suggested *V. mertensi* may display different daily behaviour to other Australian varanids. Currently there are no published data on the daily behaviour of *V. mertensi* thus to fill this knowledge gap is the aim of this chapter.

3.3 Aims

The specific aims of this chapter were to:

(1) describe both the experimental heating and cooling rates of *V. mertensi* in air and water, and relate these rates to daily behaviour observed in the field;
(2) describe daily variation in T_b and behaviour;
(3) describe seasonal differences in daily T_bs and behaviour; and
(4) describe the "typical" daily T_b profile and behaviour of an individual on a day in both wet and dry seasons.

3.4 Materials and methods

The daily behaviour of radio-tagged *V. mertensi* was firstly examined for individuals observed continuously during their active day. Secondly, the daily behaviour and T_b of radio-tagged individuals frequently radio-tracked during the field study was examined. Details of the methodology for conducting continuous observation days and frequent radio-tracking of individuals can be found in Chapter 2. To interpret the daily behaviour of *V. mertensi* in a physiological context an understanding of the heating and cooling rates of individuals was also required. Thermal time constants were calculated in the laboratory when moving individuals between ambient and aqueous conditions of different temperatures. Heating and cooling rates were also calculated ($°C min^{-1}$) for individuals observed basking and entering water in the field.

3.4.1 Laboratory heating and cooling constants

Thermal time constants were calculated for five *V. mertensi* of different sizes (Table 3.1). Individuals were captured during January 2003 and maintained at the School of Animal Biology (University of Western Australia). Outdoor enclosures were approximately 4 m x 4 m with basking sites and a swimming pool. Juveniles were housed in individual aquaria, approximately 70 cm x 40 cm in a controlled temperature room at 30 ºC. Juveniles were provided with an artificial light source for basking to provide a thermal gradient to 40 ºC and had access to a small pool for swimming. Individuals were fed lamb heart daily, except prior to trials when they were fasted for 48 hrs.

Table 3.1: Snout-vent length and body mass of five *V. mertensi* used in heating and cooling trials. Animal's 1 and 2 were juveniles, animal's 3, 4 and 5 were adults.

Animal	SVL (cm)	Tail (cm)	Total Length (cm)	Mass (g)
1	15	21	36	55
2	15	21	36	53
3	50	64	114	1850
4	56	76	132	2800
5	44	63	107	1550

Individuals were moved from an ambient air temperature to a higher or lower ambient temperature in air or water. Air/water temperatures were chosen to reflect 'typical' temperatures encountered by individuals in the field. T_b was measured and recorded with a temperature probe inserted into the cloaca (depth 50 mm) connected to a computer via a voltmeter. T_b was measured remotely allowing an observer to remain out of sight thus avoiding undue disturbance to animals during trials.

The first trial measured the heating times of individuals taken from ambient air at 25 ºC in a controlled temperature room (CTR) to ambient air at 35 ºC. Individuals were first held in the CTR until their body temperature was within 2 ºC of ambient. Individuals were suspended in plastic mesh (1 cm mesh squares) enclosures to avoid the possible effects of heat absorption from surfaces. Once an individual was moved from 25 ºC to 35 ºC, its T_b was recorded every minute. The trial was completed when an individual's T_b was within 2 º C of 35 ºC. At this point individuals were removed from 35 ºC and moved back to 25 ºC, where T_b was again recorded every minute until it was within 2 ºC of 25 ˚C.

The second trial was similar except individuals were moved from water at 25 ºC to ambient air at 35 ºC, then moved from ambient air at 35 ºC to water at 25 ºC.

This simulated an individual moving from the water into a warm terrestrial environment and vice versa.

The final two trials involved individuals in ambient air at 25 ºC being moved to water at 35 º C, and the reverse where individuals were moved from water at 35 ºC to ambient air at 25 ºC.

Heating and cooling rates were expressed as thermal time constants with unit minutes and taken as the reciprocal of the slope of a regression line describing the relationship between time (minutes) and ln (T_b-T_a) (°C) following the methodologies of (Bakken 1976; Boland and Bell 1980; Dzialowski and O'Conner 2001; Fraser 1985; Grigg *et al.* 1979 and Seebacher and Shine 2004). Time was set at zero when individuals were moved between different temperatures. T_b represented core body temperature of an individual (°C) and T_a the temperature of the environment (°C) into which an individual was moved. Figure 3.1 shows a regression line describing the relationship between time and ln (T_b – T_a), for an individual relocated from ambient air at 35 ºC to 25 ºC. The thermal time constant for the individual when cooled by 10 °C was 66 mins.

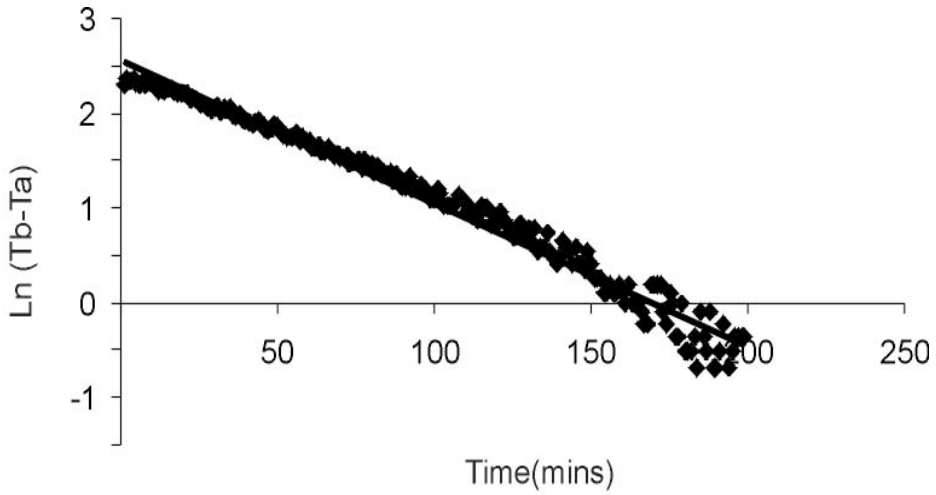


Figure 3.1: Regression relationship between time and ln (T_b – T_a) for an adult *V. mertensi* (body mass = 1150 g) moved from ambient air at 35 ˚C to 25 ˚C; equation = -0.015 (minutes) + 2.56 (r^2 = 0.97). The reciprocal of a slope of 0.015 gives a thermal time constant for the individual of 66 mins.

3.4.2 Heating and cooling rates in the field

Heating and cooling rates of individuals observed in the field were expressed simply in terms of temperature change per minute (°C min^{-1}) for individuals observed basking for more than 10 minutes in direct sunlight and submerging in water for more than 10 minutes. Heating and cooling rates measured in the field could not be expressed as thermal time constants and thus compared with laboratory-

based thermal time constants as the exact temperature of all microhabitats used by field-active individuals were not measured. Rather only a limited number of environmental temperatures were measured during field observations to give a rough estimate of temperatures available to active individuals during observations. It is appreciated that expressing field heating and cooling rates in this way does limit the comparative value of such data in that such rates are dependant on the temperature of the environment into which an individuals moves. It is envisaged, however, that this data will give an indication of the rates at which different-sized *V. mertensi* individuals can heat and cool under field conditions.

3.4.3 Active Day T_b profiles and behaviour

Active day temperature profiles and corresponding behaviour were plotted for radio-tagged individuals #17, 1.7 and 5.14. The T_b of individuals every 10 minutes and simultaneous recordings of sun, shade, ground, water temperature and the temperature of a water-filled model adult *V. mertensi* were plotted. Categorised observations of an individual's behaviour every ten minutes were plotted along a timeline bar corresponding to all temperature measurements.

Mean T_b profiles and the proportion of each hour spent behaving in each of the behavioural categories were plotted for individuals observed on multiple days. The daily T_b profile and behaviour of all *V. mertensi* was also combined and was calculated by combining T_b and behavioural data for each hour.

3.4.4 Mean midday field active core body temperature

Mean midday (MM) field active core body temperature (FAT_b) was expressed as the mean of all temperatures recorded between 11:00 - 16:00 hrs for each active individual. This expression of FAT_b follows the methodology of Christian and Weavers (1996) and allows direct comparison between the findings of the two studies. The FAT_b of individuals both observed continuously during an active day and frequently radio-tracked during the field study were calculated using this method. Mean midday temperatures of sun, shade, ground and water were also calculated using this method.

3.5 Results

Presented first in the following sections are the thermal time constants of different sized *V. mertensi* calculated in the laboratory and the heating and cooling rates of individuals observed in the field. This is followed by the daily behaviour of *V. mertensi* observed continuously during observation days. Finally the daily behaviour and T_bs of radio-tagged individuals frequently radio-located during the field study are presented.

3.6 Heating and cooling of *V. mertensi*

3.6.1 Experimental heating and cooling trials

The effect of body mass on the heating constants of different-sized *V. mertensi* when moved from ambient air at 25° C to air at 35° C was expressed by the regression equation; heating constant = 0.021(s.e = 0.003)[t < 0.01].mass(grams) + 16.3 (s.e = 5.3) [t < 0.05] (r^2 = 0.93) (Figure 3.2) and cooling constant = 0.024 (s.e = 0.004) [t < 0.01].mass (grams) + 18.9 (s.e = 6.2) [t < 0.05] (r^2 = 0.93) (Figure 3.3). This corresponds to a heating constant for a 1000g individual moved between ambient air temperatures of 37 mins and a cooling constant of 43 mins. Heating constants when moved from air to water were expressed by the regression equation; heating constant = 0.003 (s.e = 0.0004) [t < 0.01].mass (grams) + 2.3 (s.e = 0.64) [t < 0.05] (r^2 = 0.94) (Figure 3.2) and cooling constant = 0.006 (s.e = 0.002) [t < 0.05].mass (grams) + 2.6 (s.e = 2.5) [t = 0.361, ns] (r^2 = 0.823) (Figure 3.3). This corresponds to a heating constant for a 1000g individual moved between ambient air and water of 5 mins and a cooling constant of 9 mins.

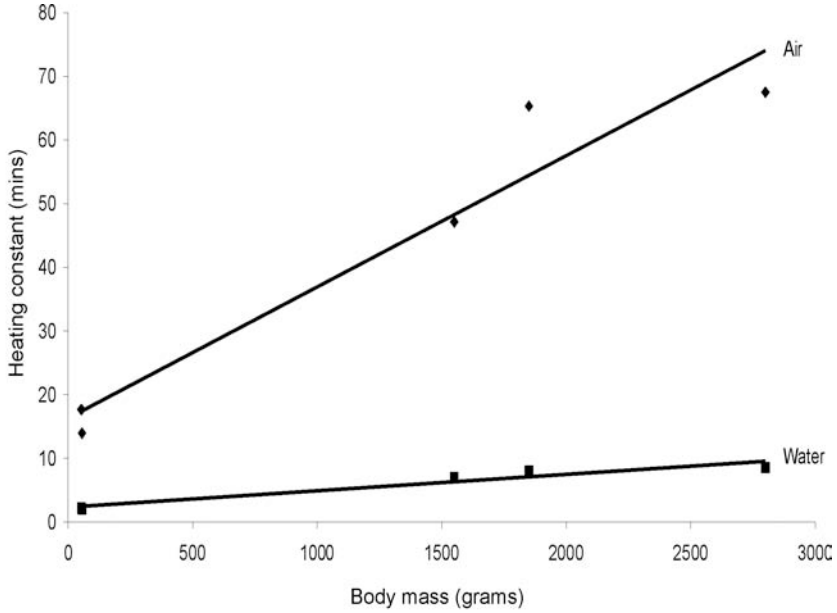


Figure 3.2: Heating constants of five different-sized *V. mertensi* moved between 25ºC and 35º C air ♦ and water ■ (see text for regression equations).

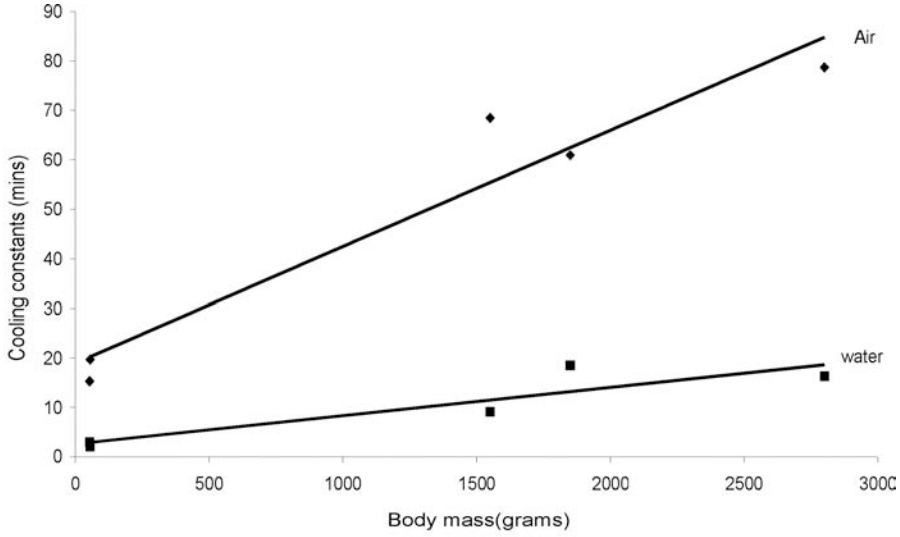


Figure 3.3: Cooling constants of five different-sized *V. mertensi* moved between 35ºC and 25º C air ♦ and water ■ (see text for regression equations).

3.6.2 Heating and cooling rates in the field

The heating rates of seven different-sized *V. mertensi*, observed basking in direct sunlight on different days, ranged from 0.02 - 0.11 °C min^{-1} (Table 3.2). The heating rate per gram of body weight of these individuals ranged from 0.000005 – 0.0001 °C $min^{-1}gram^{-1}$ (Table 3.2). The cooling rates of six different-sized *V. mertensi*, observed submerging in water on different days ranged from 0.05 – 0.19

°C min^{-1} (Table 3.3). The cooling rate per gram of body weight of these individuals ranged from 0.000006 – 0.0002 °C $min^{-1}gram^{-1}$ (Table 3.2).

Table 3.2: Heating rates for seven different-sized *V. mertensi* basking in direct sunlight for more than 10 mins. Body mass of each individual recorded on initial capture also shown.

Animal #	Date	Body mass BM (g)	T_b change (° C)	Time (mins)	Heating rate (°C min^{-1})	Heating rate per gram BM (° C $min^{-1}gram^{-1}$)
1.15	18/4/01	950	1.79	40	0.04	0.00004
17	28/4/01	1000	4.81	60	0.08	0.00008
17			1.34	30	0.04	0.00004
17			1.05	20	0.05	0.00005
17	29/5/01		4.28	50	0.09	0.00009
17	5/2/02		2.32	50	0.05	0.00005
17			0.22	30	0.06	0.00006
17	12/3/02		1.79	30	0.06	0.00006
17	19/4/02		4.14	150	0.03	0.00003
17			3.3	20	0.17	0.00017
17			1.16	70	0.02	0.00002
17	23/4/02		1.48	30	0.05	0.00005
17			1.26	20	0.06	0.00006
17	21/5/02		6.23	90	0.07	0.00007
17			4.14	20	0.21	0.00021
17			4.39	20	0.22	0.00022
17	18/6/02		9.13	70	0.13	0.00013
17			0.58	20	0.03	0.00003
17			2.76	20	0.14	0.00014
17	23/7/02		7.13	40	0.18	0.00018
17			0.46	20	0.02	0.00002
17			4.32	80	0.05	0.00005
17			1.37	20	0.07	0.00007
17	23/11/02		1.19	20	0.05	0.00005
17			0.17	30	0.005	0.000005
3.20	21/9/01	1200	2.78	30	0.09	0.000075
			1.71	30	0.06	0.00005
8	19/10/01	2150	3.2	20	0.09	0.00004
	11/10/01		2.57	30	0.09	0.00004
			0.48	20	0.02	0.000009
5.14	13/6/02	1400	3.86	120	0.03	0.00002
			1.68	30	0.06	0.00004
			1.64	30	0.05	0.00003
			2.27	40	0.06	0.00004
			1.01	20	0.05	0.00003
	14/6/02		1.92	50	0.04	0.00002
			7.81	460	0.02	0.00001
	2/7/02		13.82	60	0.23	0.0001
	31/7/02		12.83	220	0.06	0.00004
			2.61	30	0.09	0.00006
	1/8/02		17.87	240	0.07	0.00005
			2.85	30	0.1	0.00007
	30/11/02		0.14	20	0.007	0.000005
			0.6	20	0.03	0.00002
5.16	16/1/03	1200	1.85	50	0.04	0.00003
			2.17	20	0.11	0.00009
			2.25	20	0.11	0.00009
	20/1/03		3.79	20	0.19	0.00015
1.7	31/1/03	1250	0.2	10	0.02	0.000016

Table 3.3: Cooling rates for six different-sized *V. mertensi* submerging in water for more than 10 mins. Body mass of each individual on initial capture also shown.

Animal #	Date	Body mass (g)	T_b change (° C)	Time (mins)	Mean °C min^{-1}	Heating rate per gram BM (° $Cmin^{-1}gram^{-1}$)
1.15	18/4/01	950	3.26	30	0.11	0.0001
			1.01	20	0.05	0.00005
			4.12	20	0.21	0.0002
8	19/10/01	2150	3.27	20	0.16	0.00007
			0.45	30	0.015	0.000006
			0.68	20	0.03	0.00001
			0.58	20	0.03	0.00001
	10/12/01		0.37	20	0.02	0.000009
17	5/2/02	1000	6.51	60	0.11	0.0001
			4.36	50	0.09	0.00009
			2.54	40	0.06	0.00006
			1.58	20	0.08	0.00008
	12/3/02		2.38	70	0.03	0.00003
			0.6	30	0.02	0.00002
			4.04	30	0.13	0.00013
			2.28	20	0.11	0.00011
	19/4/02		0.91	60	0.02	0.00002
			0.18	20	0.009	0.000009
			1.65	30	0.06	0.00006
			2.29	10	0.23	0.00023
			3.96	20	0.198	0.0002
	23/4/02		0.26	10	0.02	0.00002
			1.17	10	0.117	0.00012
			0.67	10	0.067	0.00007
			4.29	20	0.22	0.00022
			3.24	60	0.05	0.00005
	21/5/02		3.82	30	0.13	0.00013
			2.5	50	0.05	0.00005
			2.05	10	0.21	0.00021
			4.25	10	0.43	0.00043
	18/6/02		3.61	30	0.12	0.00012
			8.27	20	0.41	0.00041
	23/7/02		2.46	50	0.05	0.00005
			2.33	20	0.12	0.00012
			3.38	10	0.34	0.00034
			3.88	60	0.06	0.00006
	23/11/02		1.94	10	0.194	0.0002
			1.49	110	0.01	0.00001
5.14	13/6/02	1400	3.5	10	0.35	0.00025
			1.17	10	0.12	0.00008
			2.99	40	0.07	0.00005
			0.68	10	0.07	0.00005
			1.16	10	0.12	0.00008
	7/2/02		4.24	40	0.12	0.00008
			7.25	30	0.24	0.00017
	31/7/02		5.81	10	0.6	0.00043
	1/8/02		1.89	10	0.19	0.00014
			2.72	10	0.27	0.0002
	30/11/02		0.49	10	0.049	0.00004
5.16	16/1/03	1200	5.37	30	0.18	0.00013
			3.9	10	0.39	0.00032
			3.36	40	0.08	0.00006
			2.44	10	0.24	0.0002
			6.36	50	0.13	0.0001
			3.37	90	0.04	0.00003
	20/1/03		2.74	40	0.07	0.00005
			3.37	80	0.04	0.00003
			1.39	30	0.05	0.00004
1.7	31/1/03	1250	0.91	40	0.02	0.00002
			1.33	20	0.07	0.00006

3.7 Continuous daily observations of radio-tagged *V. mertensi*

Data from 25 observation days of active *V. mertensi* are presented in the following sections. Owing to difficulties in observing different individuals, some were observed on multiple occasions (Table 3.4). For example, animals 17, 8 and 5.14 were observed repeatedly in both seasons. Animals 5.16 and 1.7 were observed repeatedly during the wet season and animals 1.15 and 3.20 were observed each for one day during the dry season. Data for individuals observed on multiple occasions are not statistically independent, which limits the statistical validity of some types of analysis that can be undertaken. For this reason the following sections takes a more descriptive approach to developing an understanding of the daily T_bs and behaviour of *V. mertensi* observed.

Following an overview of seasonal differences in ambient temperatures data from multiple observations of the same individuals over closely spaced days are presented to highlight day-to-day variation in both daily T_b and behaviour of individuals. This is followed by data collected from different observation days of an individual (#17) in each season allowing an examination of differences between days and seasonal variation in its T_b and behaviour. Seasonal differences identified for this individual are then further examined by considering its T_b and behaviour during a 'typical' wet and dry season day.

To further highlight seasonal differences in behaviour and T_b, the daily behaviour and field active T_b (FAT_b) of the seven different *V. mertensi* are examined. Finally, data from all observation days for all *V. mertensi* observed are combined to provide a general pattern of seasonal differences in behaviour and T_b of *V. mertensi*. However, in doing this it is recognised that different observation days of the same individuals do not represent independent samples. Despite this it is envisaged these combined data will show general trends outlining seasonal differences in the T_b and behaviour of all *V. mertensi* examined.

Table 3.4: Sixteen complete (C) days of observations of active *V. mertensi* (emergence – retreat). Nine partial (P) days of observations completed also shown. Sites where observations undertaken also shown including; Packsaddle Main Irrigation Channel (PSMIC), Ivanhoe Plains Main Irrigation Channel (IPM1) and Salerno Gorge (SG).

Animal #	Days	Date	Observation	Season	Site
17	3	5/2/02	C	Wet	PSMIC
		12/3/02	P	"	PSMIC
		23/11/02	P	"	PSMIC
5.16	2	16/1/03	P	"	IPM1
		20/1/03	P	"	IPM1
1.7	3	29/1/03	C	"	PSMIC
		31/1/03	C	"	PSMIC
		2/2/03	P	"	PSMIC
8	1	10/12/01	P	"	IPM1
5.14	1	30/11/02	P	"	SG
5.14	5	13/6/02	C	Dry	SG
		14/6/02	C	"	SG
		2/7/02	C	"	SG
		31/7/02	C	"	SG
		1/8/02	C	"	SG
17	6	28/4/01	C	"	PSMIC
		29/5/01	P	"	PSMIC
		19/4/02	C	"	PSMIC
		23/4/02	C	"	PSMIC
		21/5/02	C	"	PSMIC
		18/6/02	C	"	PSMIC
		23/7/02	C	"	PSMIC
3.20	1	21/9/01	P	"	PSMIC
8	1	19/10/01	C	"	IPM1
1.15	1	18/4/01	C	"	PSMIC

3.7.1 Seasonal variation in ambient temperatures

Mean hourly temperatures in the water, sun, ground and shade were calculated for both wet and dry season continuous observation days of radio-tagged *V. mertensi* (Figure 3.4). Water and ground temperatures were significantly higher for all hours of the day during the wet season (Tables 3.5 and 3.6). Water temperature was approximately 10 °C higher during the wet season whereas ground temperature was approximately 5 °C higher (Figure 3.4). Temperature in the sun was significantly higher during the wet season for the hours of 06:00 -11:00, 16:00 and 17:00. Temperature in the sun was 2-10 °C higher during the wet season for these hours (Table 3.7, Figure 3.4). Temperature in the shade was significantly higher during the wet season for all hours except 17:00 hrs (Table 3.8). Temperature in the shade was approximately 10 °C higher during the wet season (Figure 3.4).

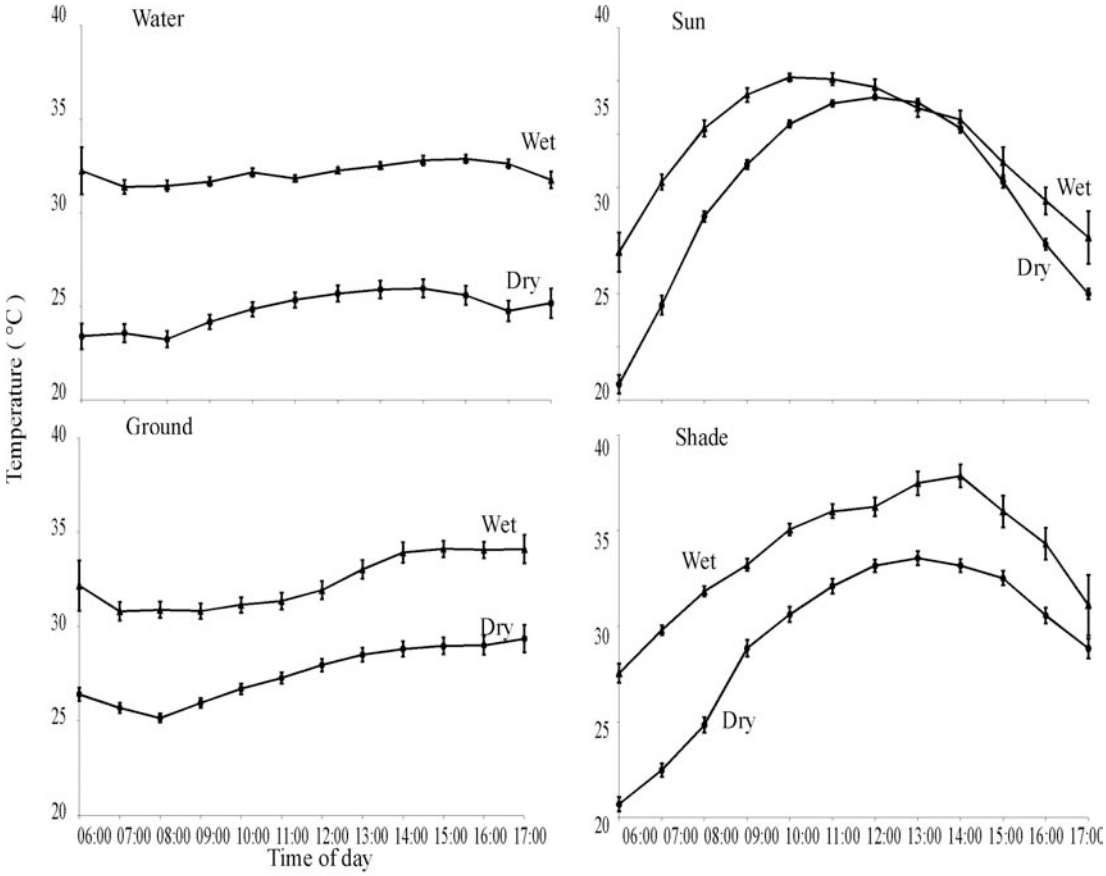


Figure 3.4: Mean hourly temperatures of water at a depth of 100 cm, full sunlight, ground at a depth of 15cm and full shade. Mean ± 1 SEM for a total of ten wet season days and fifteen dry season days.

Table 3.5: Comparison of ground temperature taken every ten minutes for each hour of the day during the wet and dry season. Ground temperature was significantly higher during the wet season for all hours of the day. Mean hourly ground temperature ± SEM shown for each season.

Hour	Mean T_{ground} (wet) ° C	SEM	Mean T_{ground} (dry) ° C	SEM	*t*	n	P
6:00	32.17	1.33	26.42	0.36	4.187	34	< 0.01
7:00	30.81	0.50	25.70	0.27	9.015	89	< 0.0001
8:00	30.90	0.44	25.17	0.23	11.530	120	< 0.0001
9:00	30.82	0.40	25.96	0.27	10.105	150	< 0.0001
10:00	31.15	0.41	26.70	0.28	9.226	155	< 0.0001
11:00	31.35	0.45	27.28	0.31	7.654	146	< 0.0001
12:00	31.93	0.48	28.01	0.34	6.750	140	< 0.0001
13:00	33.03	0.49	28.51	0.37	7.074	131	< 0.0001
14:00	33.92	0.54	28.82	0.40	8.514	123	< 0.0001
15:00	34.11	0.43	28.97	0.44	8.321	115	< 0.0001
16:00	34.06	0.43	29.00	0.50	7.713	100	< 0.0001
17:00	34.54	0.70	29.36	0.73	5.121	34	< 0.0001

Table 3.6: Comparison of water temperature taken every ten minutes for each hour of the day during the wet and dry season. Water temperature was significantly higher during the wet season for all hours of the day. Mean hourly water temperature ± SEM shown for each season.

Hour	Mean T_{water} (wet) ° C	SEM	Mean T_{water} (dry) ° C	SEM	*t*	n	P
6:00	32.24	1.26	23.40	0.69	5.910	34	< 0.0001
7:00	31.38	0.37	23.57	0.49	12.811	89	< 0.0001
8:00	31.43	0.29	23.24	0.43	15.711	120	< 0.0001
9:00	31.66	0.24	24.17	0.38	16.639	150	< 0.0001
10:00	32.16	0.22	24.84	0.39	16.217	155	< 0.0001
11:00	31.82	0.17	25.34	0.41	14.575	146	< 0.0001
12:00	32.26	0.15	25.71	0.44	14.022	140	< 0.0001
13:00	32.51	0.19	25.90	0.47	13.050	131	< 0.0001
14:00	32.80	0.26	25.95	0.48	12.941	123	< 0.0001
15:00	32.88	0.23	25.59	0.50	13.218	115	< 0.0001
16:00	32.61	0.24	24.75	0.54	13.289	100	< 0.0001
17:00	31.38	0.25	25.17	0.79	7.490	34	< 0.0001

Table 3.7: Comparison of sun temperature taken every ten minutes for each hour of the day during the wet and dry season. Sun temperature was significantly higher during the wet season for all hours of the day except 12:00 – 15:00 hrs. . Mean hourly sun temperature ± SEM shown for each season.

Hour	Mean T_{sun} (wet) ° C	SEM	Mean T_{sun} (dry) ° C	SEM	*t*	n	P
6:00	33.90	1.85	21.47	0.89	6.290	34	< 0.0001
7:00	40.50	0.72	28.91	0.91	9.990	89	< 0.0001
8:00	45.55	0.77	37.28	0.50	9.039	120	< 0.0001
9:00	48.72	0.66	42.14	0.43	8.360	150	< 0.0001
10:00	50.36	0.37	45.96	0.36	8.107	155	< 0.0001
11:00	50.20	0.57	47.91	0.30	3.547	146	< 0.001
12:00	49.43	0.75	48.52	0.26	1.143	140	ns
13:00	47.46	0.83	48.00	0.32	0.608	131	ns
14:00	46.37	0.87	45.58	0.46	0.641	123	ns
15:00	42.36	1.41	40.55	0.59	1.184	115	ns
16:00	38.74	1.27	34.64	0.53	2.975	100	< 0.01
17:00	35.40	2.81	29.98	0.52	1.893	34	<0.05

Table 3.8: Comparison of shade temperature taken every ten minutes for each hour of the day during the wet and dry season. Shade temperature was significantly higher during the wet season for all hours of the day except 17:00 hrs. . Mean hourly shade temperature ± SEM shown for each season.

Hour	Mean T_{Shade} (wet) ° C	SEM	Mean T_{shade} (dry) ° C	SEM	t	n	P
6:00	27.54	0.51	20.68	0.37	8.804	34	< 0.0001
7:00	29.80	0.25	22.47	0.36	16.691	89	< 0.0001
8:00	31.83	0.27	24.84	0.40	14.621	120	< 0.0001
9:00	33.21	0.32	28.85	0.44	8.013	150	< 0.0001
10:00	35.06	0.30	30.61	0.40	8.886	155	< 0.0001
11:00	36.02	0.36	32.10	0.39	7.299	146	< 0.0001
12:00	36.26	0.49	33.21	0.33	5.285	140	< 0.0001
13:00	37.49	0.63	33.56	0.36	5.768	131	< 0.0001
14:00	37.86	0.60	33.17	0.35	5.638	123	< 0.0001
15:00	36.01	0.83	32.51	0.38	3.842	115	< 0.001
16:00	34.31	0.82	30.56	0.42	4.059	100	< 0.001
17:00	31.21	1.80	28.84	0.53	1.263	34	ns

3.7.2 Day-to-day variation in T_b and behaviour

To show day-to-day variation in T_b and behaviour of individuals, the following sections describe the daily T_bs and behaviour of three individuals 17, 1.7 and 5.14 observed on closely spaced days.

Animal #17

Animal #17, continuously observed throughout two separate days four days apart in the dry season of 2002, showed appreciable differences in T_b, behaviour and retreat time. This individual emerged from its overnight burrow into the water at similar times on the two days (06:40 hrs on the 19/4/02 and 06:30 hrs on the 23/4/02) but retreated two hours later at 17:50 hrs on the 19/4/02 than at 15:50 hrs on the 23/4/02. Upon emergence from the water to bask at 08:30 hrs on the 23/4/02, T_b did not reach 30 ° C until 10:00 hrs (Figure 3.5). The individual's behaviour alternated between basking and swimming 7 times on the 19/4/02 and 10 times on the 23/4/02. As the individual was active for two hours more on the 19/4/02 this shows the individual moved less between the water and terrestrial environment over this active day. Behavioural observations indicated the individual spent longer periods swimming and basked less often on the 19/4/02 compared to the 23/4/02. Shade and model temperature were noticeably lower on the 23/4/02 (Figure 3.5). Shade temperature did not surpass the T_b of the individual until approximately 09:00 hrs on the 23/4/02 whereas it did so at approximately 08:30 hrs on the 19/4/02 (Figure 3.5). Lower ambient temperatures on the 23/4/02 were reflected in the lower T_bs, more periods of basking, less lengthy swimming periods and the earlier retreat time of animal #17 on the 23/4/02 compared to on the 19/4/02.

Animal # 1.7

Animal #1.7, continuously observed throughout two separate days two days apart in the wet season of 2003, showed appreciable differences in T_bs, emergence times and behaviour. The individual emerged 150 minutes later at 09:50 hrs on the 29/1/03 than on the 31/1/03. The individual began swimming upon emergence at 07:20 hrs on the 31/1/03, whereas it did not emerge and begin swimming until 09:50 hrs on the 29/1/03 (Figure 3.6). On the 29/1/03 the individual swam throughout its

active day until retreat, whereas on the 31/1/03 it swam until 14:00 hrs after which it emerged and basked twice before retreating (Figure 3.6). Sun and model temperature fell suddenly at approximately 08:30 hrs on the 29/1/03 and approximately 10:30 hrs on the 31/1/03 (Figure 3.6). Shade temperature did not begin to fall until approximately 16:00 hrs on the 29/1/03, whereas it began falling much earlier at approximately 13:30 hrs on the 31/1/03 (Figure 3.6). This fall in ambient temperature in the late afternoon on the 31/1/03 was reflected in the emergence of the individual to bask for two periods in this afternoon prior to its retreat. Emergence to bask coincided with shade temperature falling below the T_b of the individual on the 31/1/03. Alternatively on the 29/1/03 the individual may have remained in the water throughout the afternoon, when shade, model and sun temperature were substantially higher than its T_b (Figure 3.6) in an attempt to keep cool.

Animal # 5.14

Animal #5.14, observed continuously throughout two consecutive days in the dry season of 2002 showed appreciable differences in T_b, behaviour and emergence times. The individual emerged 120 minutes later on the 31/7/02 than on the 1/8/02. Before emergence on the 31/7/02 the individual warmed at a similar rate to the model until 08:30 hrs suggesting the individual was exposed to direct sunlight within its unsighted burrow (Figure 3.7). The individual emerged when its T_b fell below shade temperature at 09:20 hrs on the 31/7/02. Upon emerging the individual swam for an extended period of 60 minutes before emerging to bask until 15:50 hrs, after which it swam and basked briefly once more before retreating. While basking throughout the middle of the day the T_b of the individual fell below shade temperature on two occasions at 11:50 hrs and 16:00 hrs (Figure 3.7) on the 31/7/02. On the 1/8/02 the individual emerged after a period of constant T_b in its burrow at 07:20 hrs. It then swam for 10 minutes before emerging to bask until 15:20 hrs, after which it swam and basked briefly for two more periods before retreating (Figure 3.6). In contrast to the 31/7/02 its T_b did not fall below shade temperature while basking throughout the middle of the day (Figure 3.7). These differences show this individual remained active in the water during the morning of the 31/7/02 for longer before emerging to bask than on the 1/8/02. This difference reflects differences in morning T_b prior to emergence on the two days with the higher pre-emergence T_b of the individual prolonging aquatic activity on the morning of the 31/7/02.

Environmental and ambient temperatures recorded on the two consecutive days were similar throughout the day (Figure 3.7).

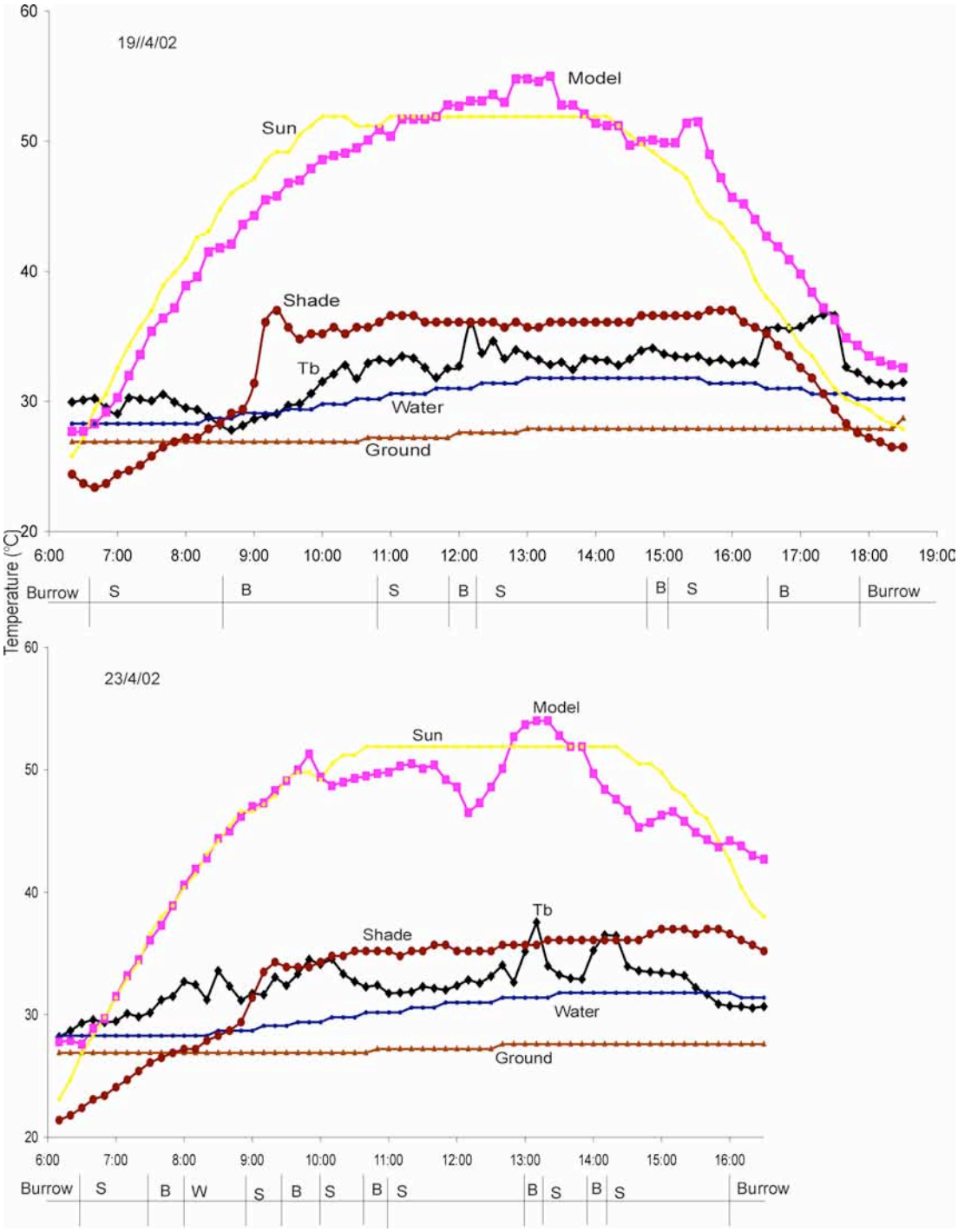


Figure 3.5: Daily T_b and behaviour of animal #17 recorded at ten minute intervals on two days during the early dry season of 2002 in the Packsaddle Main Irrigation Channel. Simultaneous temperature recordings of sun, shade, water, ground and temperature of a water filled model adult *V. mertensi* also shown. Timeline shows behaviour, S = swimming, B = basking and W = walking throughout the day. Emergence occurred at 06:40 and retreat at 17:50 hrs on the 19/4/02 and 06:30 and 15:50 hrs on the 23/4/02.

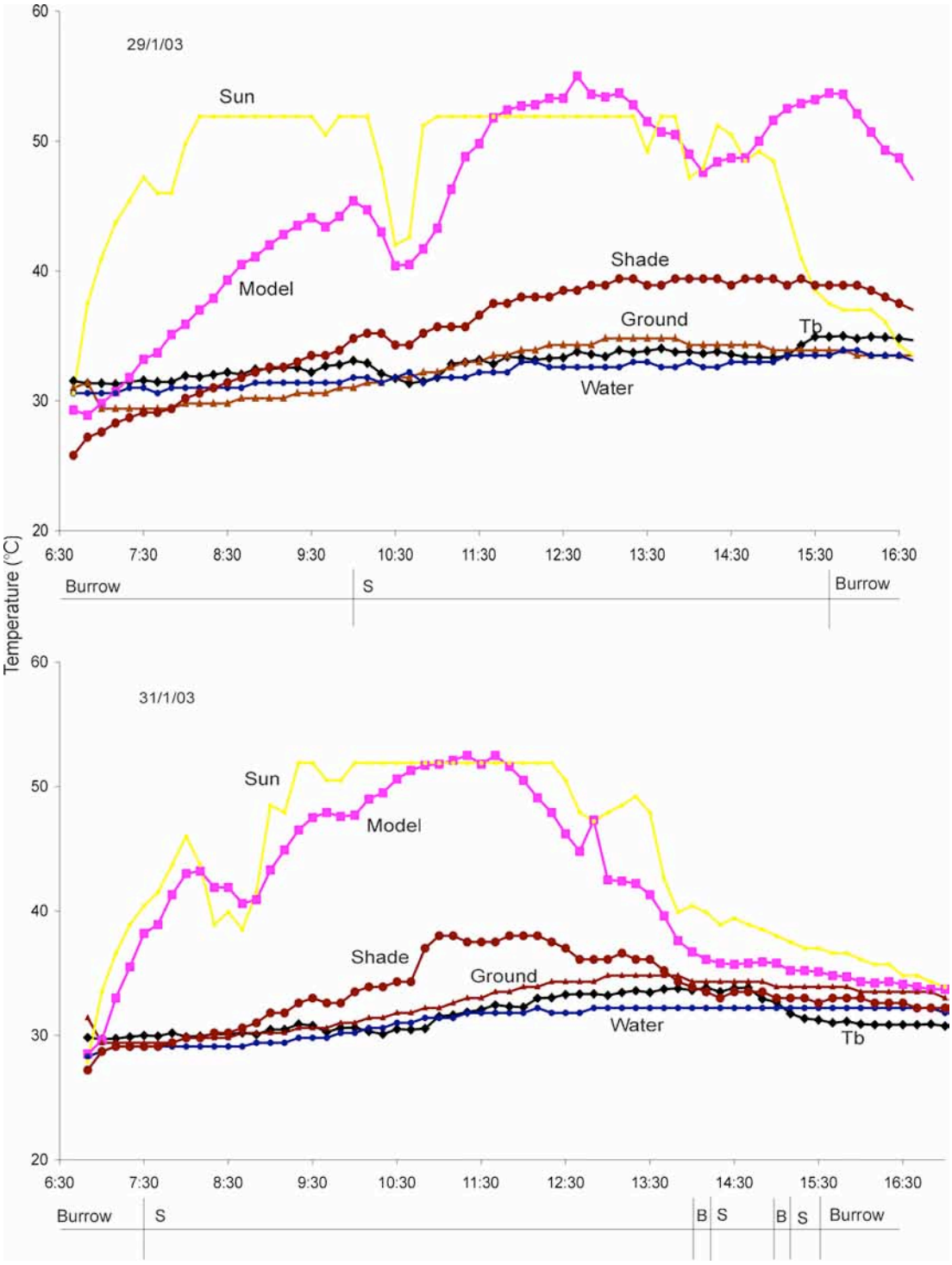


Figure 3.6: Daily T_b and behaviour of animal #1.7 recorded at ten minute intervals on two days during the late wet season of 2003 in a farm dam adjacent the Packsaddle Main Irrigation Channel. Simultaneous temperature recordings of sun, shade, water, ground and temperature of a water filled model adult *V. mertensi* also shown. Timeline shows behaviour, S = swimming, B = basking and W = walking. Emergence occurred at 09:50 and retreat at 15:40 hrs on the 29/1/03 and 07:20 and 15:30 hrs on the 31/1/03.

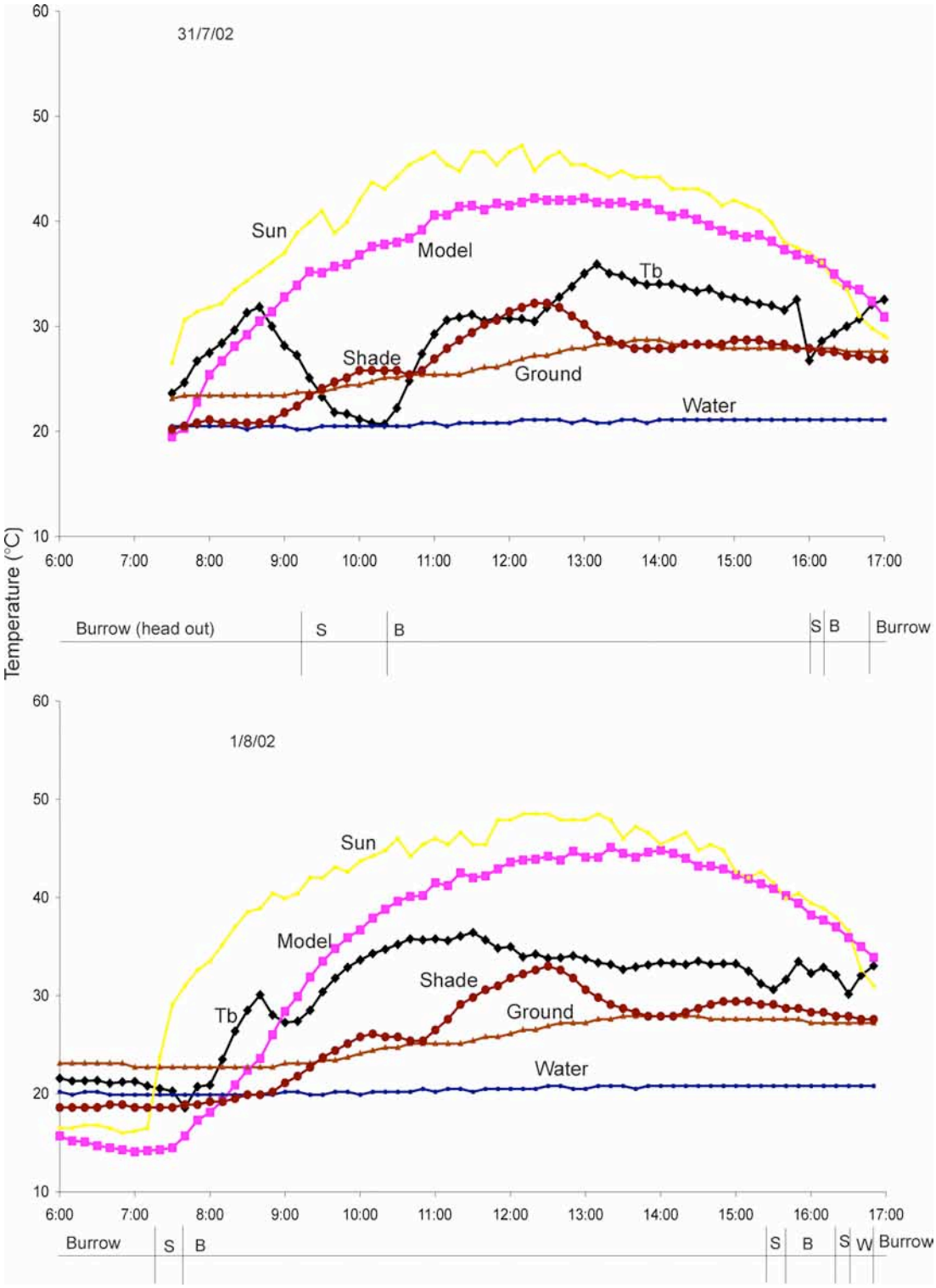


Figure 3.7: Daily T_b and behaviour of animal #5.14 recorded at ten minute intervals on two days during the late dry season of 2002 in the main pool of Salerno Gorge. Simultaneous temperature recordings of sun, shade, water, ground and temperature of a water filled model adult *V. mertensi* also shown. Timeline shows behaviour, S = swimming, B = basking and W = walking. Emergence occurred at 09:20 and retreat at 16:40 hrs on the 31/7/02 and 07:20 and 16:50 hrs on the 1/8/02.

3.7.3 T_b and behaviour of animal #17

Seasonal variation in mean daily T_b and behaviour

To show seasonal differences in daily T_b and behaviour the following sections firstly describes the mean daily T_b and behaviour of one radio-tagged *V. mertensi* (animal #17) observed continuously on 8 different days during the dry season and 3 days during the wet season. To expand on seasonal differences identified in mean daily T_b and behaviour, a 'typical' wet season and dry season day are also presented.

The mean daily T_b profile of animal # 17 was higher during the wet than the dry season for all hours of the day (Figure 3.8). T_b during the wet season ranged between 33-36 ° C, whereas during the dry season T_b was between 26 – 32 ° C. During the dry season, T_b remained above water temperature by as much as 5 ° C throughout an active day (07:00 – 16:00 hrs), whereas during the wet season T_b was similar to water temperature for all active hours (07:00 – 16:00 hrs), except 06:00, 11:00 and 12:00 hrs. T_b during the hours of 06:00 and 07:00 hrs in the dry season was similar to ground temperature while during the wet season T_b was higher for these hours (Figure 3.8). Further highlighting seasonal differences in ambient temperatures, outlined in previous sections, all ambient temperatures recorded during the 8 dry season days on which animal #17 was observed were lower than those recorded on the 3 wet season days (Figure 3.8).

Animal # 17 basked during the dry season for a greater or equal proportion of time than it swam for all hours except 07:00 and 13:00 hrs (Figure 3.8). In contrast, it swam for a greater or equal proportion of time for all hours except 06:00 hrs during the wet season (Figure 3.8). It was observed foraging in all hours between 07:00 – 16:00 hrs during the dry season and all hours between 06:00 – 12:00 during the wet season except 10:00 hrs (Figure 3.8).

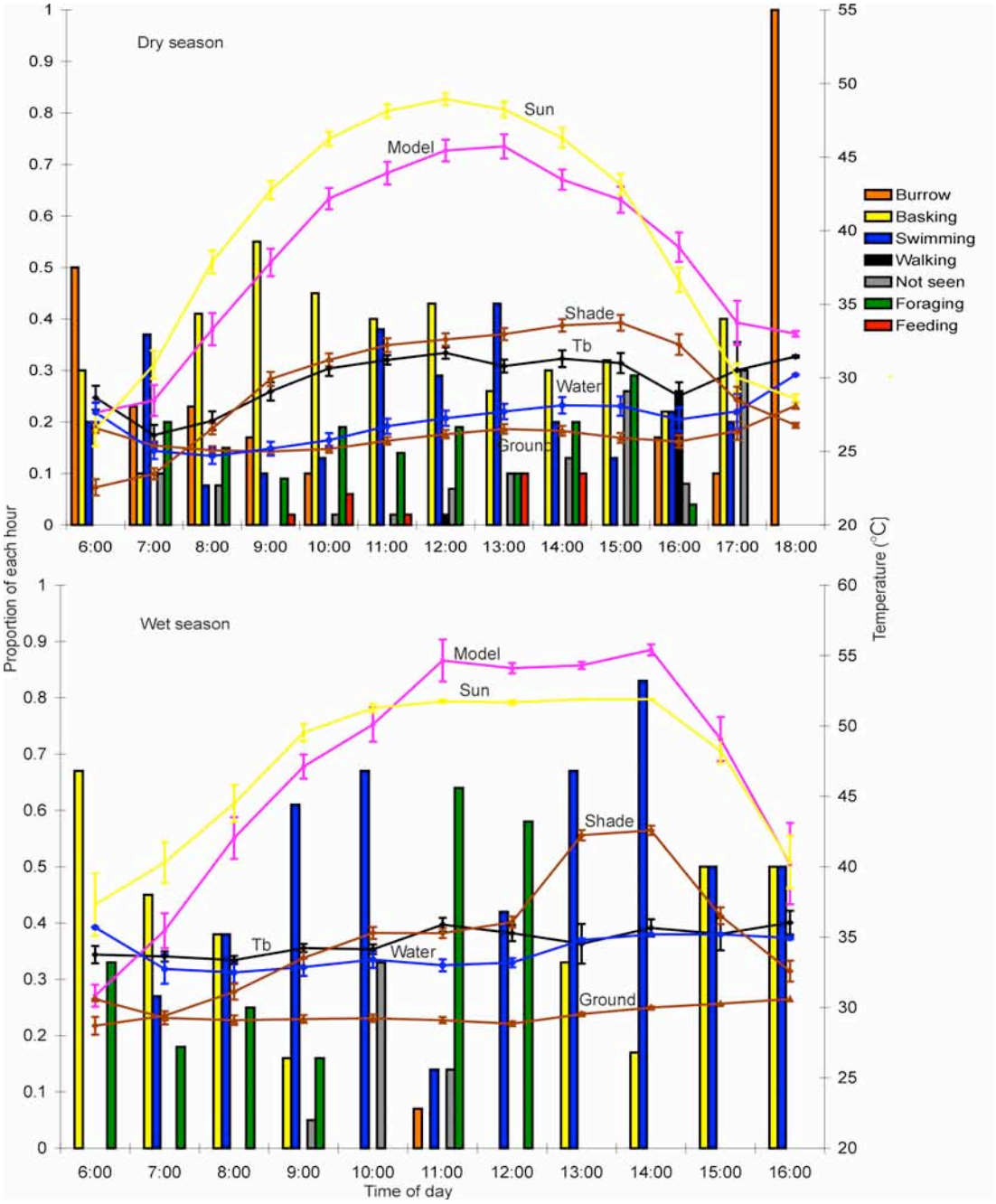


Figure 3.8: Mean hourly T_b of animal # 17 recorded at ten minute intervals for a total of 8 dry season and 3 wet season continuous observation days. Simultaneous temperature recordings of sun, shade, water, ground and temperature of a water filled model adult *V. mertensi* shown. Proportion of each hour an individual observed behaving in each behavioural category also shown (behavioural categories, see Chapter 2).

Variation between a 'typical' wet and dry season day

The T_b of animal #17 on a "typical" dry season day showed a morning 'warm up period' whereby the individual basked increasing it's T_b by approximately 11 °C between 08:00 - 09:15 hrs (Figure 3.9). Following this, T_b fluctuated throughout the remainder of the day, between 25 - 32 °C and approximately 5- 10 °C higher than water temperature which was between 20 - 22 °C (Figure 3.9). A "typical" wet

season day showed a slower increase in T_b during the morning 'warm up period' whereby animal #17 basked increasing T_b by only 3 °C between 08:20 - 09:15 hrs. T_b also fluctuated throughout the remainder of the wet season day between 32 and 40 °C compared to between 25 and 32 °C during the dry season day. In contrast to during the dry season day, these T_bs were only slightly above water temperature which ranged from 31- 34 °C (Figure 3.9).

The dry season day showed 12 cycles of fluctuating T_b (temperature gain through basking and loss through swimming) between 09:30 - 17:00 hrs (Figure 3.9). In contrast, there were only five such cycles between 10:00 - 17:00 on the wet season day (Figure 3.9). It was observed basking for six periods totalling 360 minutes and swimming for six periods totalling 140 minutes on the dry season day (Figure 3.9). In contrast, it was observed basking for four periods totalling 140 minutes and swimming for five periods totalling 290 minutes on the wet season day (Figure 3.9). Overall, animal # 17 basked for longer and emerged from the water to bask more regularly on the dry season day compared to the wet season day. Alternatively, it spent more time swimming and emerged from the water to bask less on the wet season day.

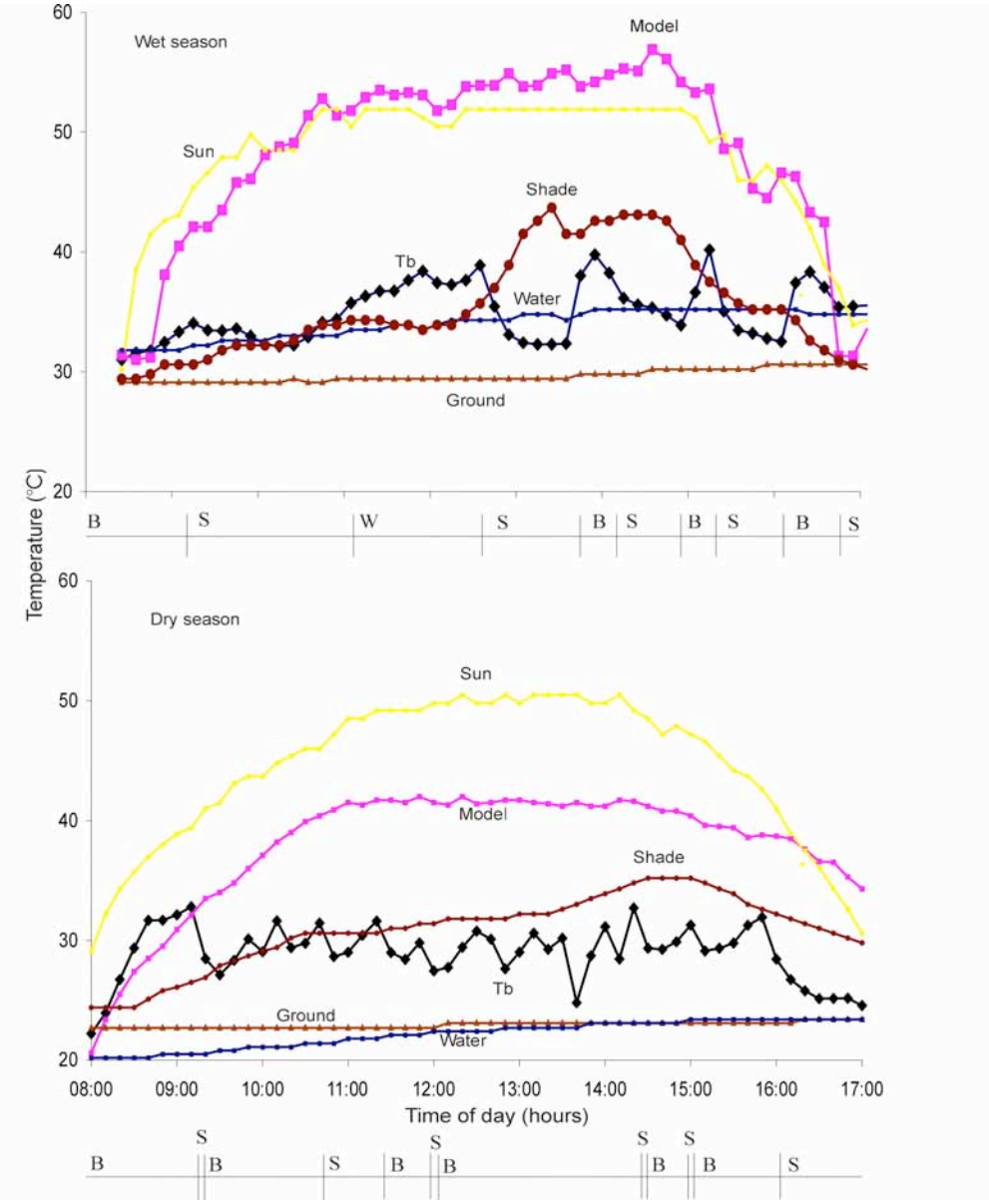


Figure 3.9: T_b of animal #17 recorded at ten minute intervals on a wet season day (5/2/02) with emergence at 08:25, retreat at 16:55 hrs, and on a dry season day (23/7/02) with emergence at 08:00, retreat at 17:00 hrs. Simultaneous temperature recordings of sun, shade, water, ground and the temperature of a water filled model adult *V. mertensi* also shown. Timelines show corresponding behaviour on both days; B = basking, S = swimming and W = walking.

3.7.4 Emergence/retreat times, behaviour and field active midday T_b

Emergence and retreat times

Mean emergence and retreat times, Western Standard Time (WST) can be seen in Table 3.9. Earliest emergence from an overnight refuge burrow during the dry season was 07:20 hrs. Latest retreat time during this season was 17:00 hrs. Earliest emergence during the wet season was 06:30 hrs and latest retreat 17:50 hrs. On four occasions individuals retreated in the early morning or middle of the day (Table 3.9). In these instances individuals were not seen to resume their activity that

day. In all cases these retreats resulted from individuals being disturbed. On nine occasions the emergence time of individuals was not recorded as individuals could not be located until after emergence. Similarly, on two occasions the retreat time was not recorded as individuals were not observed retreating.

Behaviour

Varanus mertensi observed in irrigation watercourses spent 2.9 times as long basking during the dry season compared to the wet season (Table 3.10). Individuals spent 1.9 times as long swimming during the wet season compared to the dry season. Individuals spent five times as long foraging whilst swimming during wet season compared to the dry season (Table 3.10).

Table 3.9: The emergence and retreat times (WST) of six *V. mertensi* observed on different days in the two seasons. Italics indicate retreat due to disturbance; such times were excluded from calculations of means. N represents number of different individuals included in calculation of means.

Animal #	Date	Season	Emergence time	Retreat time
17	23/11/2002	Wet		*11:10*
17	5/2/2002	Wet		16:55
8	10/12/2001	Wet		*12:15*
5.14	30/11/2002	Wet		*9:10*
5.16	16/1/2003	Wet		17:00
5.16	20/1/2003	Wet		16:50
1.7	29/1/2003	Wet	9:50	15:40
1.7	31/1/2003	Wet	7:20	15:30
1.7	2/2/2003	Wet		16:20
Mean			8:05	16:33
n			1	3
SEM				20 mins
17	19/4/2002	Dry	6:40	17:50
17	23/4/2002	Dry	6:30	15:30
17	21/5/2002	Dry	7:10	
5.14	13/6/2002	Dry	8:30	16:30
5.14	14/6/2002	Dry	7:50	
5.14	31/7/2002	Dry	9:20	16:40
5.14	1/8/2002	Dry	7:20	16:40
5.14	2/7/2002	Dry		16:50
3.20	21/9/2001	Dry		15:20
8	24/4/2001	Dry	9:15	*9:45*
Mean			8:05	16:09
n			3	3
SEM			48 mins	26 mins

Table 3.10: Time and percentage (shown in parentheses) of total active time spent behaving in different ways by six *V. mertensi*. Site of observation and mean percentage of total active time spent behaving in different ways by all *V. mertensi* also shown.

Animal	**Date**	**Season**	**Site**	**Basking time (mins)**	**Swimming time (mins)**	**Foraging (swimming) time (mins)**	**Foraging (walking) time (mins)**	**Walking time (mins)**	**Not seen time (mins)**	**Total active time (mins)**
17	28/4/01	1	PS channel	110 (34.3)	130 (40.6)	0 (0)	0 (0)	80(25)	0 (0)	320
17	29/5/01	1	PS channel	110 (35.4)	30 (9.7)	0 (0)	0 (0)	179 (54.8)	0 (0)	310
17	19/4/02	1	PS channel	250 (39)	190 (29.7)	170 (26.5)	30 (4.6)	0 (0)	0 (0)	640
17	23/4/02	1	PS channel	100 (19.2)	100 (19.2)	270 (51.9)	40 (7.6)	10 (1.9)	0 (0)	520
17	21/5/02	1	PS channel	310 (66)	160 (34)	0 (0)	0 (0)	0 (0)	0 (0)	470
17	18/6/02	1	PS channel	140 (37.8)	230 (62.1)	0 (0)	0 (0)	0 (0)	0 (0)	370
17	23/7/02	1	PS channel	390 (70.9)	150 (27.3)	0 (0)	0 (0)	10 (1.8)	0 (0)	550
17	23/11/02	2	PS channel	60 (23)	140 (53.8)	40 (15.4)	20 (7.6)	0 (0)	0 (0)	260
17	5/2/02	2	PS channel	50 (9.6)	50 (9.6)	0 (0)	30 (5.7)	0 (0)	390 (75)	520
17	12/3/02	2	PS channel	40 (11.4)	140 (40)	30 (8.5)	50 (14)	0 (0)	90 (25.7)	350
Mean (dry)				**43.2 %**	**31.8 %**	**11.2 %**	**1.7 %**	**11.9%**	**0 %**	
Mean (wet)				**14.7 %**	**34.5 %**	**8 %**	**9.1%**	**0 %**	**33.6%**	
1.7	29/1/03	2	PS channel	0 (0)	120 (35.3)	220 (64.7)	0 (0)	0 (0)	0 (0)	340
1.7	31/1/03	2	PS channel	20 (4.1)	270 (56.3)	190 (39.5)	0 (0)	0 (0)	0 (0)	480
1.7	2/2/03	2	PS channel	0 (0)	570 (100)	0 (0)	0 (0)	0 (0)	0 (0)	570
Mean (wet)				**1.4 %**	**63.9 %**	**34.7 %**	**0 %**	**0 %**	**0 %**	
8	19/10/01	1	M1 channel	180 (**54.5**)	90 (**27.3**)	10 (**3**)	40 (**12**)	10 (**3**)	0 (**0**)	330
8	10/12/01	2	M1 channel	70 (**58.3**)	10 (**8.3**)	20 (**16.7**)	0 (**0**)	20 (**16.7**)	0 (**0**)	120
5.16	16/1/03	2	M1 channel	130 (21.7)	250 (41.7)	180 (30)	10 (1.7)	30 (5)	0 (0)	600
5.16	20/1/03	2	M1 channel	30 (5.1)	480 (82.8)	0 (0)	0 (0)	70 (12)	0 (0)	580
Mean (wet)				**13.4 %**	**62.3 %**	**15 %**	**0.9 %**	**8.5 %**	**0 %**	
3.20	21/9/01	1	PS channel	30 (**60**)	20 (**40**)	0 (**0**)	0 (**0**)	0 (**0**)	0 (**0**)	50
1.15	18/4/01	1	PS channel	280 (**56**)	90 (**18**)	0 (**0**)	0 (**0**)	130 (**26**)	0 (**0**)	500
Mean (dry)				**53 %**	**21.4 %**	**3.6 %**	**3.4 %**	**10.2 %**	**0 %**	
Mean (wet)				**18 %**	**42.3 %**	**18.6 %**	**2.5 %**	**6.3 %**	**8.4 %**	
n				**4**	**4**	**4**	**4**	**4**	**4**	
5.14	13/6/02	1	Salerno gorge	440 (95.7)	10 (2.1)	0 (0)	0 (0)	10 (2.1)	0 (0)	460
5.14	14/6/02	1	Salerno gorge	520 (100)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	520
5.14	2/7/02	1	Salerno gorge	70 (31.8)	120 (54.5)	0 (0)	0 (0)	30 (13.6)	0 (0)	220
5.14	31/7/02	1	Salerno gorge	360 (80)	80 (17.8)	0 (0)	0 (0)	10 (2.2)	0 (0)	450
5.14	1/8/02	1	Salerno gorge	500 (90.9)	40 (7.2)	0 (0)	0 (0)	10 (1.8)	0 (0)	550
5.14	30/11/02	2	Salerno gorge	40 (44.4)	50 (55.5)	0 (0)	0 (0)	0 (0)	0 (0)	90
Mean (dry)				**79.7 %**	**16.3 %**	**0 %**	**0 %**	**3.9 %**	**0 %**	
Mean (wet)				**44.4 %**	**55.5 %**	**0 %**	**0 %**	**0 %**	**0 %**	

Midday field active T_b (FAT_b)

The FAT_b (11:00 – 16:00 hrs) for seven *V. mertensi* are shown in Table 3.11. Of these individuals, the FAT_b of two individuals (#17 and #8) was calculated for both seasons. The mean FAT_b of two remaining animals (#1.7 and 5.16) during the wet season was 34 °C. This was only slightly higher than the mean FAT_b of three remaining animals (#5.14, 3.20 and 1.15) during the dry season of 33.3 ± 1.2 °C.

Of the two individuals for which FAT_b was calculated for both seasons, animal #17 had a mean FAT_b of 35.2 °C (n = 2 days) during the wet and 31.3 ± 0.9 °C (n = 7 days) during the dry. Animal #8 had a FAT_b of 32.4 °C (n = 1 day) during the wet and 31.5 °C (n = 2 days) during the dry.

Table 3.11: The FAT_b of seven *V. mertensi* continuously observed on multiple days during both wet and dry seasons. Number of observation days completed and mean FAT_b ± SEM also shown.

Animal #	**n (days)**	**Season**	**Mean midday FA T_b**
17	2	Wet	35.79
			34.61
Mean			**35.20**
5.16	2		33.19
			33.22
Mean			**33.21**
1.7	3		33.63
			32.67
			34.82
Mean			**33.71**
SEM			**0.6**
8	1		**32.40**
5.14	5	Dry	34.45
			33.71
			28.28
			32.39
			33.64
Mean			**32.49**
SEM			**1.1**
17	7		32.15
			31.85
			33.32
			33.23
			32.07
			26.54
			29.54
Mean			**31.25**
SEM			**0.9**
3.20	1		**31.69**
8	2		27.95
			35.10
Mean			**31.52**
1.15			**35.61**

3.7.5 Combined T_bs and behaviour of all *V. mertensi*

Seasonal variation in active day T_b

To further illustrate seasonal differences in daily T_b and behaviour, data for all continuous observation days of all radio-tagged *V. mertensi* (Table 3.5) were combined in the following sections. This presumes multiple observation days of the same individual are statistically independent which is not necessarily the case. Accordingly, limited statistical analysis is undertaken on these combined data and appropriate caution taken in interpreting these results.

Combined mean T_bs were 2-5 °C higher during the wet season than the dry season for all hours of the day (Figure 3.10). Similarly, the temperature of a water filled model adult *V. mertensi* was 5-10 °C higher between 06:00 – 12:00 hrs and 2-3 ° C higher between 13:00 – 17:00 hrs during the wet compared to the dry season (Figure 3.10).

Combined mean T_bs showed *V. mertensi* underwent a 'morning warm up period' during both seasons between 07:00 and 11:00 hours (Figure 3.10). During the wet season mean T_b increased by 2 °C from 31.6 °C at 07:00 hrs to 33.6 °C at 11:00 hrs. In comparison T_b increased by approximately 3 times as much, increasing by 6.1 °C from 26.1 °C at 07:00 hrs to 32.2 °C at 12:00 hrs during the dry season. Mean T_b remained relatively constant between 11:00 – 16:00 hrs during both seasons until, at approximately 16:00 hours, T_b began to fall (Figure 3.10). T_bs between 11:00 – 16:00 hrs were 1.5 °C higher during the wet season ranging from 33.5 – 34.0 °C compared to 32.0 - 32.5 °C during the dry season (Figure 3.10).

Dry season active day T_bs and ambient temperatures

Combined mean daily T_bs were lower than the temperature in the sun and the temperature of the model for all hours except 06:00 and 07:00 hrs during the dry season (Figure 3.11). In contrast, T_b was higher than water temperature for all hours (Figure 3.11). T_b was higher than temperature in the shade between 06:00 – 11:00 hrs, lower between 11:00 – 14:00 hrs, similar between 14:00 – 16:00 hrs and higher during the hour of 17:00 (Figure 3.11). T_b was similar to ground temperature for the hours of 06:00, 07:00 and 17:00 hrs (Figure 3.11).

Wet season active day T_bs and ambient temperatures

Combined mean daily T_bs were lower than the temperature of sun and the model for all hours except 06:00 hrs during the wet season (Figure 3.11). T_b was higher than water temperature for all hours except 06:00 – 08:00, 16:00 and 17:00 hrs when temperatures were similar (Figure 3.11). T_b was lower than shade temperature for the hours of 10:00 – 16:00 hrs, similar for 08:00, 09:00, 16:00 and 17:00 hrs and higher for 06:00 and 07:00 hrs (Figure 3.11). T_b was similar to ground temperature for 06:00 – 08:00 hrs and 14:00 and 15:00 hrs, higher for the hours of 09:00 – 13:00 hrs and lower for the hours of 16:00 and 17:00 hrs (Figure 3.11).

Exploitation of experimental set point temperature range

Combined mean T_bs during the dry season did not reach the minimum experimental preferred temperature range of *V. mertensi* of 33.1 °C determined by (Christian and Weavers 1996). Alternatively, during the wet season mean T_b fell within this range for a total 6 hrs between 11:00 – 16:00 hrs (Figure 3.11).

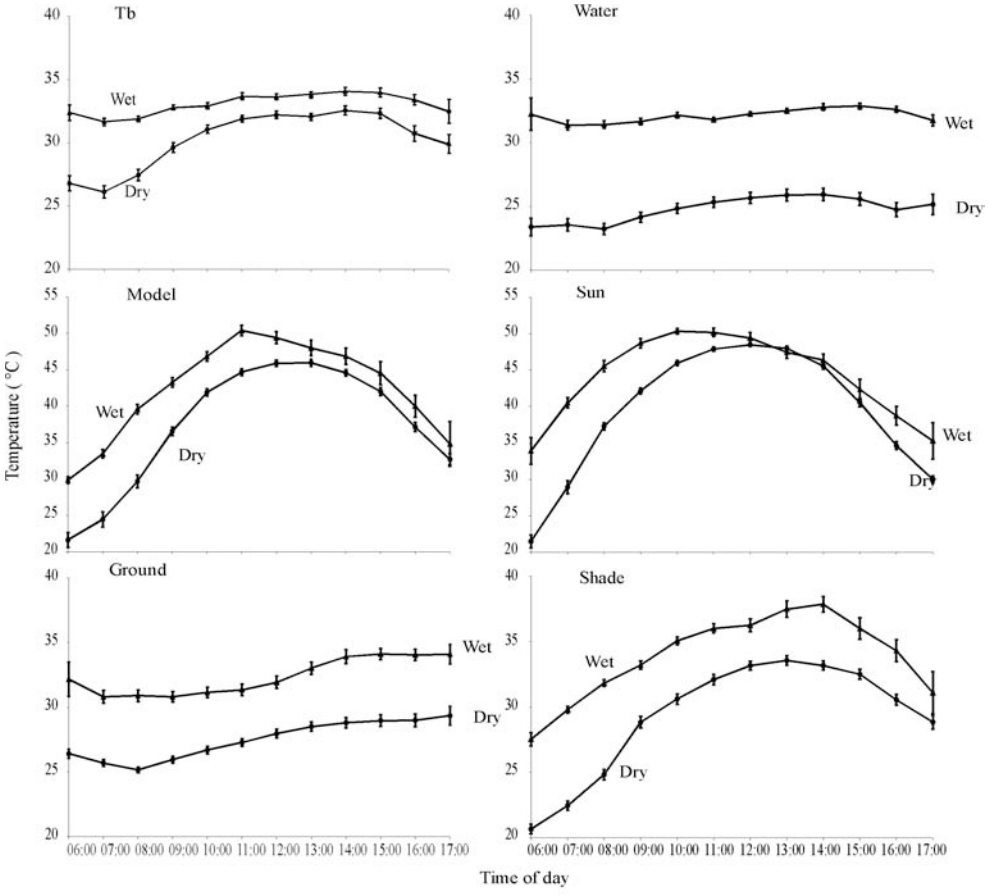


Figure 3.10: Combined mean hourly T_b of *V. mertensi* for all observation days. Mean hourly temperatures of sun, shade, ground, water and the temperature of a water-filled model adult *V. mertensi* also shown.

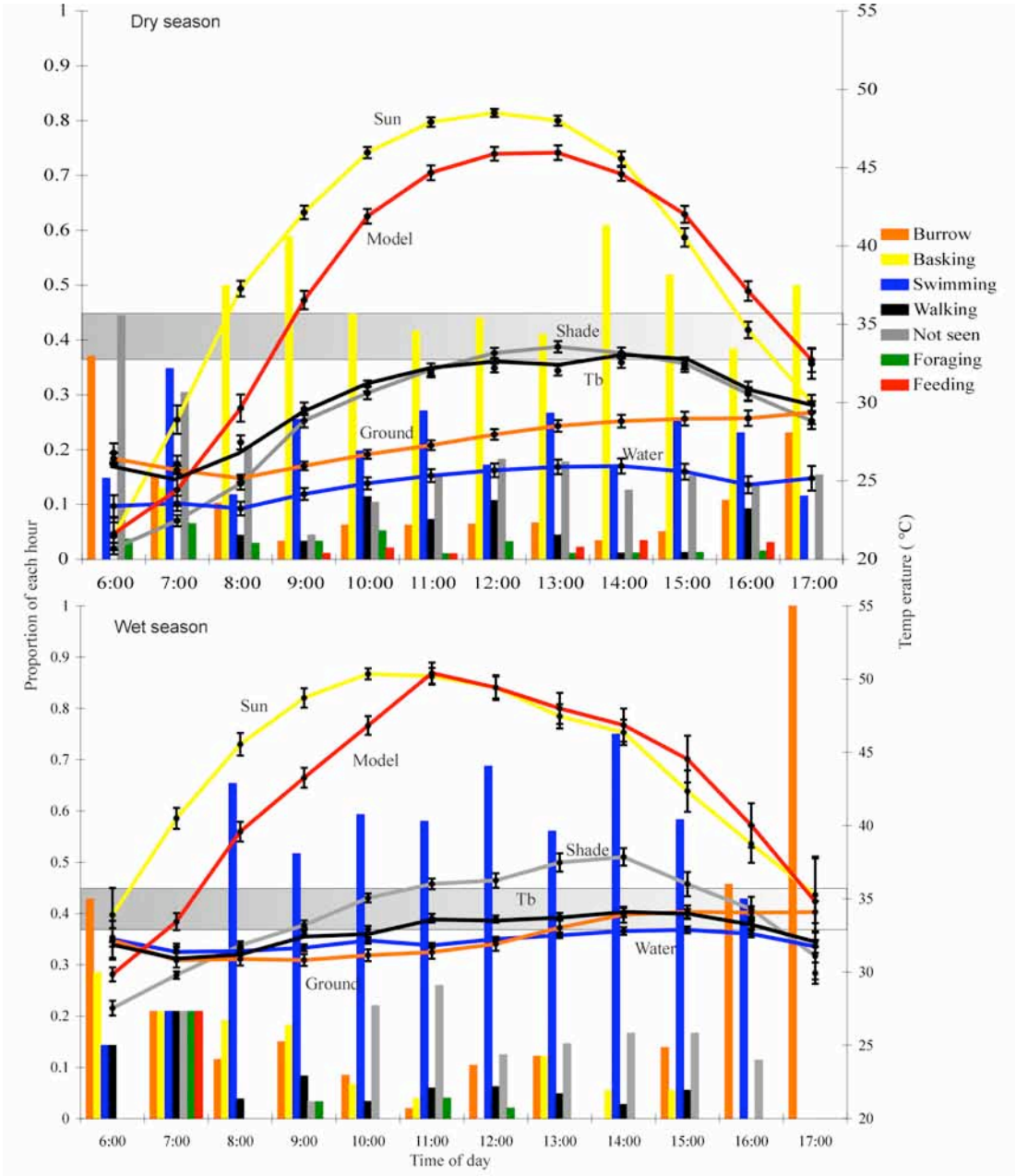


Figure 3.11: Mean hourly T_b taken at 10 minute intervals combined for all observation days of radio-tagged *V. mertensi* ± SEM. Mean hourly temperature recordings of sun, shade, ground, and water and the temperature of a water filled model *V. mertensi* taken simultaneously at 10 minute intervals during observation days ± SEM. Mean proportion of each hour observed individuals spent behaving in different behavioural categories also shown (see Chapter 2 for behavioural categories). Shaded area depicts the experimental preferred set point temperature range of *V. mertensi* of 33.1 – 35.5 ° C (Christian and Weavers 1996).

Wet season behaviour

Combined data from all observation days indicated *V. mertensi* spent proportionally more time swimming during the wet season in all hours except for 06:00, 07:00 and 17:00 hrs (Figures 3.11). During 06:00 and 17:00 hrs individuals were found predominantly in their burrows. During 07:00, individuals evenly

proportioned their time between all seven behaviours (Figure 3.11). Individuals foraged in all hours between 07:00 -12:00 hrs except during the hour of 10:00 during the wet season (Figure 3.11).

Dry season behaviour

During the dry season *V. mertensi* spent more time basking than swimming for all hours except 6:00 and 7:00 hrs when they spent more time swimming (Figure 3.11). Individuals foraged in all hours between 06:00 – 16:00 hrs during the dry season.

3.7.6 T_b and behaviour of frequently radio-tracked *V. mertensi*

In addition to T_b and behaviour data collected during days when radio-tagged individuals were continuously observed, similar data were also collected from active radio-tagged *V. mertensi* frequently radio-tracked during the field study. This larger dataset, with a high number of independent samples, enables a more robust statistical analysis of seasonal differences in T_b and behaviour.

A total of 17 radio-tagged *V. mertensi* were frequently radio-tracked during dry season months. A further 17 radio-tagged *V. mertensi* were frequently radio-tracked during wet season months. The mean midday FAT_b of each radio-tagged *V. mertensi* was calculated by taking the mean of all T_b recordings taken between 11:00 – 16:00 hrs for each season. Only mean midday FAT_b values for each *V. mertensi* were considered in the following analysis (Table 3.12). Similarly, only mean midday environmental temperatures calculated from all temperature recordings between 11:00 -16:00 hrs were considered.

3.7.7 Seasonal variation in ambient temperatures

Mean midday shade temperature was significantly higher during the wet season ($t_{33} = 3.502$, $P < 0.01$) as was ground temperature ($t_{33} = 3.568$, $P < 0.01$) and water temperature ($t_{33} = 3.427$, $P < 0.01$, Table 3.12). Mean midday sun temperatures were not different during the two seasons ($t_{33} = 0.795$, ns, Table 3.12).

3.7.8 Field active T_b

The mean midday FAT_b of *V. mertensi* observed while actively *walking, swimming, basking, foraging* or *not seen but known to be active* upon radio-location during the wet season was significantly higher than during the dry season ($t_{33} = 3.241$, $P < 0.01$) (Table 3.12). Mean midday FAT_b was higher than water temperature during both the dry ($t_{33} = 4.75$, $P < 0.0001$) and wet ($t_{33} = 3.15$, $P < 0.01$) seasons (Table 3.12). Mean midday FAT_b was also higher than ground temperature during the dry season ($t_{33} = 2.75$, $P < 0.05$), however, was similar during the wet season ($t_{33} = 1.83$, ns, Table 3.12). Mean midday FAT_b was lower than the temperature in the sun during both the dry ($t_{33} = 5.8$, $P < 0.0001$) and wet ($t_{33} = 4.9$, $P < 0.0001$) seasons (Table 3.12). Mean midday FAT_b was also lower than the temperature in the shade during both the dry ($t_{33} = 3.6$, $P < 0.01$) and wet ($t_{33} = 4.5$, $P <0.01$) seasons (Table 3.12).

3.7.9 Behaviour

Fifty eight observations of the 17 radio-tagged *V. mertensi* frequently radio-tracked were made between 11:00 – 16:00 hrs during dry season months. On 29 (48%) of these occasions individuals were observed basking/walking, on 17 (28%) occasions individuals were observed swimming and on 12 (20%) occasions individuals were not seen but known to be active. Seventy six observations of radio-tagged *V. mertensi* frequently radio-tracked were made between 11:00 – 16:00 hrs during wet season months. On 9 (12%) of these occasions individuals were observed basking/walking, on 9 (12%) occasions individuals were observed swimming and on 58 (76%) occasions individuals were not seen but known to be active. Considering only observations of *V. mertensi* swimming and basking there was no significant difference in the amount of time spent basking and swimming during the two seasons ($\chi_1^2 = 0.913$, ns).

During the field study the behaviour of many radio-located individuals was recorded as ‘not seen but known to be active’ as indicated by a moving radio signal. In most cases this resulted from difficulties in observing individuals active in water. It would thus seem appropriate to consider observations of individuals ‘active but not seen’ as individuals ‘swimming’. If the above data are re-analysed replacing observations of individuals ‘not seen but known to be active’ with individuals ‘swimming’ then individuals would have been observed swimming for 50% and

basking/walking for 50 % of observations recorded during the dry season. Alternatively individuals would have been observed swimming for 88% of observations and basking/walking for only 12% of observations during the wet season. These adjusted data show that *V. mertensi* swam significantly more and basked less during the wet season compared to the dry season (χ_1^2 = 25.78, P < 0.001).

Table 3.12: Mean midday (MM) FAT_b of *V. mertensi* radio-located during both seasons. Simultaneously recorded MM temperature of sun, shade, water and ground also shown.

#	Season	MM FAT_b	MM shade temperature	MM sun temperature	MM water temperature	MM ground temperature
1	Dry	31.9	35.8	40.7	27.0	29.3
1.14	Dry	31.8	34.3	36.6	25.0	26.1
1.16	Dry	32.7	39.6	44.7	33.5	35.7
1.8	Dry	33.3	33.0	36.9	21.5	20.1
2.6	Dry	29.6	31.9	33.8	26.4	29.1
2.8	Dry	29.5	32.4	35.8	23.1	27.0
3.17	Dry	33.7	35.9	35.9	30.0	30.0
4.11	Dry	29.7	34.1	36.6	26.2	27.2
4.16	Dry	30.3	33.0	37.8	25.9	29.1
4.18	Dry	29.4	31.7	39.7	24.0	28.3
4.9	Dry	26.9	33.9	35.2	22.5	23.3
5.16	Dry	31.9	39.9	44.1	28.8	32.4
6	Dry	31.7	31.8	32.9	23.2	24.5
8	Dry	35.2	34.9	38.1	28.6	29.8
12	Dry	27.8	32.9	34.3	25.1	26.9
17	Dry	34.6	34.8	34.9	31.9	33.9
18	Dry	31.1	31.2	32.6	28.9	28.5
Grand Mean		31.3	34.2	37.1	26.6	28.3
SEM		0.6	0.6	0.9	0.8	0.9
n		17	17	17	17	17
1.13	Wet	33.8	39.0	38.5	31.6	33.1
1.7	Wet	34.1	37.3	40.4	31.4	35.4
2	Wet	31.6	37.9	33.5	30.3	32.0
2.13	Wet	28.9	34.7	36.1	30.3	32.0
3.14	Wet	34.0	35.5	37.7	30.0	30.0
3.16	Wet	33.5	42.8	39.3	30.0	30.0
3.18	Wet	34.8	43.7	39.3	32.3	33.2
3.19	Wet	34.2	45.8	40.8	34.5	36.3
4	Wet	33.9	38.7	35.8	34.0	35.8
4.14	Wet	34.0	37.0	38.6	31.0	32.7
4.6	Wet	35.4	39.3	40.6	34.8	30.5
5.14	Wet	34.8	31.1	33.8	19.6	27.4
5.18	Wet	33.0	42.7	47.5	28.9	33.1
7	Wet	30.7	34.2	35.2	27.3	29.5
11	Wet	33.6	37.4	37.6	32.0	33.6
15	Wet	33.0	41.7	38.6	31.4	32.3
20	Wet	35.5	32.1	33.5	30.0	30.0
Grand Mean		33.5	38.3	38.0	30.5	32.1
SEM		0.4	1.0	0.8	0.8	0.6
n		17	17	17	17	17

3.8 Discussion

3.8.1 Temperatures experienced by active *V. mertensi*

The temperatures of sunlight, shade, ground and water experienced by active *V. mertensi* during the wet season were all significantly higher than during the dry season. Of perhaps greatest importance to *V. mertensi* that spend 61% and 25% of their active day in the water during the wet and dry season respectively is a seasonal difference in water temperature. Dry season water temperatures ranged between 23 - 26° C compared to between 31- 33°C during the wet season. Dry season water temperature is below the experimental preferred T_b range of *V. mertensi* of between 27 - 31° C. This may limit aquatic activity during the dry season. The effects of aquatic activity on the T_b of *V. mertensi* may thus be pivotal in shaping the daily the behaviour of *V. mertensi* during the dry season.

3.8.2 Heating and cooling of *V. mertensi*

Varanus mertensi generally had similar heating and cooling time constants to other comparable sized varanids during experimental trials under ambient air conditions (Table 3.13, Figure 3.12). Heating and cooling time constants increased with body mass something that has been widely reported in other varanids (Bartholomew and Tucker 1964; Brattstrom 1973; Earll 1982; Grigg *et al.* 1979; Heger 2000; King *et al.* 1991; King *et al.* 1989; King 1991; McNab and Auffenberg 1976; Meek 1978). This reflects the greater thermal inertia of large varanids compared to smaller conspecifics. In the field, the high thermal inertia of large *V. mertensi* would allow such individuals to maintain elevated T_bs for longer when entering cold water. This may limit the amount of aquatic foraging undertaken by small *V. mertensi* compared to larger conspecifics.

More widely, a similar effect of body mass on thermal time constants has been proposed for all ‘lizard-shaped’ reptiles excluding Chelonia and Snakes (Grigg *et al.* 1979). Grigg *et al.* (1979) presented several formulas for predicting thermal time constants based on body mass for ‘lizard-shaped’ reptiles including; for heating in air ln(thermal constant) = 0.72 + 0.36.ln.mass (grams); heating in water ln(thermal constant) = -2.11 + 0.61.ln.mass (grams); cooling in air ln(thermal constant) = 0.42 + 0.44.ln.mass (grams) and cooling in water ln (thermal constant) = -2.07 + 0.66.ln.mass (grams). These formulas give comparable heating times for ‘lizard-

shaped' reptiles to those predicted by formulae presented in the study for *V. mertensi*. For example, a 1000g 'lizard-shaped' reptile would be expected to take 24 mins to heat by 10°C in air compared to 37 mins for *V. mertensi*, 8 mins compared to 5 mins for *V. mertensi* to heat in water, 32 mins compared to 43 mins for *V. mertensi* to cool in air and 12 mins compared to 9 mins for *V. mertensi* to cool in water. This suggests the heating and cooling rates of *V. mertensi* are similar to those predicted for all 'lizard-shaped' reptile taxa excluding Chelonia and snakes by Grigg et al. (1979).

Varanus mertensi heated and cooled considerably faster in water than in air during laboratory trials. This shows that activity in water, at a different temperature to the T_b of an individual, quickly alters T_b. Similarly Meek (1978) showed that *V. salvator* had a noticeably reduced T_b after entering cold water. Given the extent of aquatic activity undertaken by *V. mertensi* and the rapid effects of water temperature on T_b, water temperature is of considerable importance in shaping the daily behaviour of *V. mertensi*. For example, prompt cooling of individuals foraging in cold water necessitates emergence to bask and re-elevate fallen T_b before resuming aquatic foraging. This suggests *V. mertensi* may incur a cost of foraging in cold water through reduced foraging time and increased exposure to predators while basking to regain lost T_b. *Varanus mertensi* observed submerging in water in the field also cooled rapidly at rates up to 0.19 °C min^{-1}. This further highlights the rapid effects of cold water on the T_b of individuals supporting the findings of laboratory trials. Rapid cooling rates have also been reported for *V. salvator* observed in field entering water (Traeholt 1995). This again highlights the importance of water temperature and its affects on T_b in shaping the behaviour of both semi-aquatic species.

Varanus mertensi observed basking in the field also heated rapidly at rates of up to 0.11 °C min^{-1}. High heating rates most likely reflect basking sites used in the field which provide convective and radiant heat gain to basking individuals. The high solar absorbance of *V. mertensi* may also aid in rapid heat gain when basking in direct sunlight. The high solar absorbance of individuals has been suggested as advantageous for the semi-aquatic *V. mertensi*, allowing prompt regain of lost T_b when basking after emerging from cold water (Christian *et al.* 1996). This is supported by the observations of this study which showed individuals basking after emerging from cold water quickly elevate their T_b allowing them to promptly resume their aquatic activity. This high solar-absorbance, facilitating rapid regain of lost T_b,

may aid in counteracting the costs incurred through activity in cold water such as reduced foraging time and increased exposure to predators.

Table 3.13: Heating and cooling constants for five *V. mertensi* compared to other varanids. Constants calculated for all individuals moved between ambient air conditions differing by 10°C. NB: Data for other species adopted from (Heger 2000).

Species	Mass(g)	Heating constant	Cooling constant
V.acanthurus	16	7.87	6.99
V. mertensi	**53**	**17.63**	**15.29**
V. mertensi	**55**	**13.92**	**19.68**
V. gouldii	94	12.82	13.51
V. giganteus	99	13.00	16.80
V. gouldii	144	10.87	13.16
V. tristis	186	14.08	14.93
V. gouldii	256	20.50	37.60
V. varius	735	18.87	25.64
V. gouldii	736	21.74	25.64
V. varius	774	22.73	27.03
V. gouldii	1060	25.64	35.71
V. giganteus	1215	37.20	71.40
V. mertensi	**1550**	**47.17**	**68.49**
V. bengalensis	1561	65.22	136.36
V. bengalensis	1640	83.33	125.00
V. giganteus	1834	34.60	76.90
V. mertensi	**1850**	**65.36**	**60.97**
V. bengalensis	2012	88.24	115.38
V. mertensi	**2800**	**67.57**	**78.74**
V. giganteus	2880	53.20	114.90
V. giganteus	3240	44.10	129.90
V. varius	4008	52.63	58.82
V. giganteus	5505	82.00	149.30

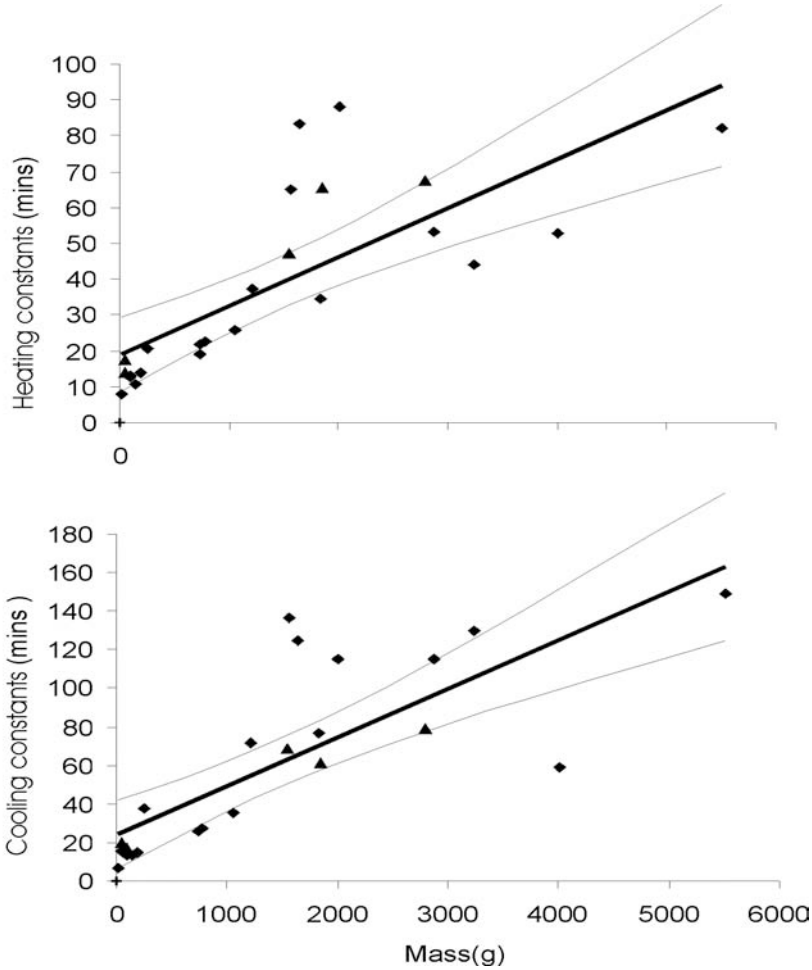


Figure 3.12: Heating and cooling constants for five *V. mertensi* ▲ and other varanids of different species ♦ (data adapted from (Heger 2000). Times calculated for individuals moved between ambient air conditions differing by 10°C. Dashed lines indicate 95% confidence limits excluding *V. mertensi* data.

3.8.3 Emergence and retreat times

The time of emergence and retreat of *V. mertensi* varied daily. Emergence times in the East Kimberley were around 06:00 hrs (WST) compared to around 08:00 (WST) in the N.T (Christian and Weavers 1996). These emergence times are also similar to those reported for other varanids. For example, the semi-aquatic *V. salvator* emerges as early as 06:00 hrs (Wikramanayake 1995; Traeholt 1995), *V. komodoensis* between 06:00 - 07:00 hrs (Wikramanayake *et al.* 1999), and *V. giganteus* between 06:00 - 08:45 hrs (King *et al.* 1989). *Varanus gouldii* and *V. rosenbergi* emerge slightly later between 07:30 - 10:30 hrs (Christian and Weavers 1994; King 1980), and *V. griseus* between 07:55 - 09:30 hrs (Ibrahim 2000).

Retreat times of *V. mertensi* in the East Kimberley of between 17:00 and 17:50 hrs (WST) were similar to those in the NT of between 16:00 hrs and 17:00 hrs (WST) (Christian and Weavers 1996). Like emergence times, the retreat times of *V.*

mertensi are similar to those of other varanids. For example, the semi-aquatic *V. salvator* retreats between 16:00 - 18:00 hrs (Wikramanayake 1995), *V. komodoensis* between 17:00 - 18:00 hrs (Wikramanayake *et al.* 1999), *V. giganteus* between 15:15 - 21:00 hrs (King *et al.* 1989) and *V. griseus* between 17:40 - 16:40 hrs (Stanner and Mendelssohn 1991). These similarities in the emergence and retreat times of *V. mertensi* and other varanids suggest further similarities in the daily T_bs and behaviour of *V. mertensi* and other semi-aquatic and terrestrial varanids.

3.8.4 T_bs, behaviour and seasonal inactivity

This study showed that daily T_b profiles of individuals varied among days. This day-to-day variation is similar to that reported for other varanids (Christian and Bedford 1995; Christian and Weavers 1996; Ibrahim 2000; King 1980; Heger 2000; Meek 1978; Thompson *et al.* 1999; Traeholt 1995; Wikramanayake 1995). Seasonal differences in mean daily T_b profiles were also evident. During the dry season, T_b generally increased quickly in the morning before remaining relatively constant throughout the day until just prior to retreat when T_b began to fall. During the wet season, T_b generally only increased slightly in the morning before remaining relatively constant throughout the day until just prior to retreat. Despite these seasonal differences, a general pattern of increasing T_b in the morning followed by relatively constant midday T_bs prior to an afternoon decline in T_b towards retreat is similar to daily T_b profiles reported for other varanids including *V. salvator* (Traeholt 1995; Wikramanayake 1995), *V. panoptes* (Christian and Weavers 1996; Christian *et al.* 1995), *V. gouldii* (Christian and Weavers 1996.; Christian *et al.* 1995; King 1980), *V. rosenbergi* (Christian and Weavers 1994; Christian and Weavers 1996), *V. tristis* (Thompson *et al.* 1999), *V. giganteus* (King *et al.* 1989; Heger 2000), *V. scalaris* (Christian and Bedford 1996) and *V. griseus* (Ibrahim 2000). The similar general daily T_b profiles of *V. mertensi* and other varanids suggests similarities in the daily behaviour of *V. mertensi* and other varanids. Specifically, *V. mertensi*, like most varanids, begin their day by basking during the morning to elevate their T_b. During the middle of the day they maintain relatively constant T_bs within a narrow temperature range before retreating in the late afternoon after their T_b begins to fall with declining ambient temperatures.

Varanus mertensi observed in this study, unlike some temperate and arid zone varanids, did not display a “midday period of reduced activity”. Rather,

observed individuals remained active throughout the day and did not seek shelter in the shade during the hot middle of the day, as do some other varanids (Pianka 1982; Pianka 1986; Pianka 1994; Pianka *et al.* 2004; Thompson 1995; Thompson 1996). The extensive aquatic activity of *V. mertensi* during its active day negates the need to seek shelter in the shade during hot midday periods when T_bs can rise to CT_{max}. Instead, individuals that enter the water after periods of terrestrial activity quickly reduce their T_b to water temperature well below CT_{max}. Use of water to cool following periods of terrestrial activity during hot midday periods has also been reported for *V. salvator* (Traeholt 1995). This suggests that semi-aquatic varanids can sustain their daily activity through aquatic activity during the heat of the day, unlike some temperate and arid zone terrestrial varanids that may need to seek shelter in cooler microhabitats, such as shade, to avoid exposure to critical thermal maximum T_bs.

In contrast to a study of *V. mertensi* in the Northern Territory by Christian and Weavers (1996), this study showed significant seasonal differences in the FAT_bs maintained by *V. mertensi*. These differences were shown to reflect seasonal differences in the behaviour of *V. mertensi* and ambient and microhabitat temperatures experienced by active individuals. A similar link between seasonal differences in ambient and microhabitat temperatures and T_bs has been reported for *V. salvator* (Traeholt 1995), *V. gouldii* (King 1980), *V. rosenbergi* (Christian and Weavers 1994; Christian and Weavers 1996), *V. scalaris* (Christian and Bedford 1996) and *V. panoptes* (Christian and Weavers 1996). Specifically, this study showed that significant seasonal differences in water temperature experienced by aquatically-active *V. mertensi* were reflected in their behaviour. For example, water temperature, close to the experimentally preferred T_b of *V. mertensi*, allowed individuals to remain in the water for longer periods during a wet season day without the need to emerge from the water and bask. In contrast, low water temperature necessitated periods of basking to elevate T_b during a dry season day. This was reflected in more time spent basking during the dry than wet season, and more time spent swimming during the wet, than the dry season. It was also evident when examining fluctuations in T_b coinciding with periods of swimming and basking by animal #17 on a 'typical' dry and wet season day.

The T_bs maintained by active semi-aquatic varanids, such as *V. salvator* and *V. mertensi*, have been reported to be lower than those of terrestrial species

(Christian and Weavers 1996; Meek 1978; Traeholt 1995; Wikramanayake 1995). The daily T_bs of *V. mertensi* examined in this study were no exception to this. Lower active T_bs are thought to reflect the highly aquatic lifestyle of semi-aquatic varanids facilitating more extensive aquatic activity in cooler aquatic microhabitats (Christian and Weavers 1996; Traeholt 1995; Wikramanayake 1995; Meek 1978). This study also showed that *V. mertensi* spent a considerable proportion of their day active in the water.

The mean daily T_bs of *V. mertensi* active in the East Kimberley during the dry season did not attain the minimum preferred experimental temperature for *V. mertensi* of 33.1 °C (Christian and Weavers 1996). This shows that *V. mertensi* can remain active during the cooler dry season while maintaining T_bs lower than their minimum experimentally preferred T_b. This allows *V. mertensi* to remain active in cooler water during the dry season where they can forage for aquatic prey resources.

This study shows that the experimental preferred temperature range determined for *V. mertensi* by Christian and Weavers (1996) does not reflect temperatures maintained by active *V. mertensi* during the dry season in the East Kimberley. Alternatively, *V. mertensi* observed in the Northern Territory did maintain T_bs within this range for a proportion of their active day (Christian and Weavers 1996). This suggests that the experimental preferred T_b range, determined in the Northern Territory, may only be applicable to *V. mertensi* within that region. In support of this, another study by Christian and Bedford (1996) of *V. scalaris* showed regional differences in the experimental preferred T_bs of individuals from different regions of tropical Australia.

A difference in the daily T_bs of active *V. mertensi* in the East Kimberley and Northern Territory may reflect a difference in microhabitat temperatures, such as water temperature, experienced by *V. mertensi* in the two regions. For example, *V. mertensi* in the East Kimberley swam in mainly fast flowing irrigation channels supplied with cold water (< 20 ° C). This cold water is pumped from a depth of approximately 20 m from the bottom of Lake Kununurra to supply both the Ivanhoe Plains and Packsaddle Plains Irrigation Areas. In contrast, *V. mertensi* examined by Christian and Bedford (1996) at Lake Bennett in the N.T swam mainly in the warm surface waters (≈ 30 ° C) of a dam above established thermoclines (Gavin Bedford, pers. comm). Similar regional differences in the microhabitats experienced by

individuals were linked with differences in the T_bs of *V. salvator* examined on Peninsula Malaysia and the island of Tulai (Traeholt 1995).

The tropical *V. mertensi* has been reported to remain active year round (Christian and Weavers 1996; Shine 1986). Unlike several Australian temperate zone varanids that have been shown to become seasonally inactive during cooler periods of the year such as *V. rosenbergi* (King 1980) and *V. gouldii* (Christian and Weavers 1996). This study showed that seasonal differences in the behaviour of *V. mertensi* facilitates activity during both seasons despite seasonal differences in ambient and microhabitat temperatures experienced by active individuals. This combined with the lower experimentally preferred T_bs of *V. mertensi* compared to other terrestrial varanids may facilitate year round activity in cooler aquatic microhabitats. This study suggests cooler dry season inactivity by *V. mertensi* in tropical Australia is unlikely to result from seasonally low temperatures inducing inactivity. This was supported by observations of numerous active individuals that were able to meet their daily temperature requirements satisfactorily during the dry season.

-Chapter 4-

The diet and foraging behaviour of *V. mertensi*

Publications resulting from this chapter

Mayes, P.J, Thompson, G.G and Withers, P.C (2005). Diet and foraging behaviour of *Varanus mertensi* (Reptilia: Varanidae). *Wildlife Research* 32: 67-74.

4.1 Summary

Dietary data and foraging observations show that *V. mertensi* is an active, opportunistic forager of aquatic and riparian environments. They consume a wide variety of relatively small vertebrate and invertebrate prey, particularly freshwater crabs, *Holthuisana* sp. However, they consume many small prey items rather than concentrating their foraging efforts on large high-energy benefit prey groups. Individuals use previous prey capture experience to maximise foraging efficiency by concentrating search efforts in areas where prey were previously captured. Individuals seldom venture far away from water in search of prey. They walk or swim slowly forward swaying their heads from side-to-side while regularly flicking their tongue when actively searching for prey. *Varanus mertensi* detect prey using both olfactory and visual stimuli in both the terrestrial and aquatic environments.

4.2 Introduction

To develop an understanding of the ecology and behaviour of any species it is important to understand its diet. Knowledge of diet gives an understanding of the ecological niche occupied by a species and allows interpretation of other behavioural and ecological traits. To describe the diet of *V. mertensi* inhabiting waterbodies of the ORIS and surrounding East Kimberley is the first aim of this chapter. This will further our understanding of the diet of *V. mertensi* across its Australian distribution and the diet of varanids in general.

Understanding how a species forages for its prey is also important in understanding the ecological niche occupied by a species. For instance, is *V. mertensi* wide ranging or sedentary, an opportunist or a specialist? The second aim of this

chapter is to describe the foraging behaviour of *V. mertensi* in waterbodies of the ORIS and surrounding East Kimberley. This will further our understanding of the foraging behaviour of semi-aquatic varanids and varanids in general.

4.2.1 Diet and foraging behaviour of varanids

Through using a variety of techniques, much information has been gathered on the diet of varanids. Substantial information on the foraging behaviour of both wild and captive varanids has also been compiled. Losos and Greene (1988) presented an extensive overview of both the diet and foraging behaviour of 35 varanid species, commenting on ecological and evolutionary implications. In their paper they concluded that most varanids are generalists with a diet comprised of a variety of small items including invertebrates and vertebrates. They do, however, note several exceptions with *V. komodoensis* and *V. bengalensis* consuming primarily large prey items. *Varanus komodoensis* and *V. bengalensis* have been reported to occasionally consume large prey several times their own body mass (Auffenberg 1981; 1983; Losos and Greene 1988). Most species of varanids are regarded as high level predators in their respective environments (Auffenberg 1981; 1994). Most have an ontogenetic shift in diet, switching from small invertebrates as juveniles to larger invertebrates and the occasional vertebrate as adults (Losos and Greene 1988). Seasonal and geographic variation in diet is also common amongst varanids (Losos and Greene 1988; Shine 1986; Thompson and King 1995).

Given the generalised diet of most varanids, Losos and Greene (1988) concluded that they are generally wide-ranging foragers that encounter many different prey groups. They also suggested that most varanids concentrate their foraging efforts in areas where high prey densities have previously been encountered. This behaviour was also reported by Shine (1986) for four sympatric species of Australian varanids. Shine (1986) reported that these species were intelligent predators that draw on previous prey capture experience to maximise their hunting efficiency. *Varanus tristis* (Thompson *et al.* 1999) and *V. gouldii* (Thompson 1995) have also been shown to draw on previous prey capture experience to maximise their hunting efficiency.

Semi-aquatic varanids also have a generalised diet. However, the diet of semi-aquatic species is often concentrated on aquatic or riparian prey groups such as fish (*V. mitchelli*) (Shine 1986), crustaceans (*V. mertensi*) (Shine 1986) (*V.*

semiremex) (Peters 1969), juvenile crocodiles and mollusks (*V. niloticus*) (Bayless 1992; Lonnberg 1903) and mollusks and crustaceans (*V. salvator*) (Gaulke 1989;1991). As for terrestrial species there are geographic, seasonal and ontogenetic differences in the diet of semi-aquatic varanids (Losos and Greene 1988). The diet and foraging behaviour of five semi-aquatic varanids has been reported in the literature; *V. salvator* consumes crustaceans (crabs) that they dig up from soil or sand burrows (Gaulke 1989; Losos and Greene 1988), fish that they capture in shallow brackish water (Gaulke 1989) and occasionally carrion on islands of the Philippines (Gaulke 1991; Traeholt 1994); *V. niloticus* consumes mainly crabs (56% of diet), slugs, snails, arthropods, newborn dwarf crocodiles and smaller conspecifics (Angelici and Luiselli 1999; Losos and Greene 1988); *V. mitchelli* consumes frogs, cicadas, fish, orthropterans, crabs, beetles, reptile eggs, birds, mice and spiders (Shine 1986) and *V. semiremex* consumes crustaceans (Brachyura) and frogs (Bustard 1970; James *et al.* 1992).

4.2.2 Diet and foraging behavior of *V. mertensi*

The diet of *V. mertensi* has been reported by Shine (1986) after examination of stomach contents from the Western Australian and Northern Territory Museums. Shine (1986) also collected and examined the stomach contents of several *V. mertensi* found near Jabiru in the Northern Territory. In the Northern Territory, *V. mertensi* were found to have a mainly aquatic diet focusing on freshwater crabs, *Holthuisana* sp. Shine (1986) also showed that *V. mertensi* rarely consume large vertebrates. The diet of *V. mertensi* collected from Jabiru differed from that of *V. mertensi* held in the Western Australian Museum collection, where the dominant prey was tree bugs rather than freshwater crabs. This suggests geographic differences in prey available to *V. mertensi* in different geographic regions across tropical Australia.

Losos and Greene (1988) also reported on the diet of *V. mertensi* from the stomach contents of two *V. mertensi* held at the American Museum of Natural History; one individual contained a crab (10 g) and a partial insect wing while a second individual contained a crab and three grasshoppers. To compare the diet of *V. mertensi* in the ORIS and surrounding East Kimberley with that already reported for other regions was the first objective of this chapter.

The foraging behaviour of *V. mertensi* is relatively unknown, with the exception of one short note describing a feeding sequence observed in the Northern Territory. This sequence described an individual herding fish in a small waterhole (Hermes 1981). The individual was seen using successive tail swipes across a pool of dimensions 3 m x 2 m to drive trapped fish into the shallow edges of the pool where they were captured and consumed. Hermes (1981) also described how one large fish (8 cm long) was carried away from the pool and consumed on the nearby bank. To expand on this limited knowledge and develop an understanding of the foraging behaviour of *V. mertensi* and varanids in general was the second objective of this chapter.

4.2.3 Techniques for examining diet

Stomach content samples taken from museum collections have been widely used to describe the diet of varanids (Losos and Greene 1988; Shine 1986). However, museum specimens are often from a large geographic distribution, over an extended time period. Stomach flushing of field-caught individuals, in a particular area, allows diet to be described within a smaller geographical area on a shorter time scale. This technique has been used to describe the diet of several varanid species in small geographical areas (Shine 1986; Thompson and King 1995; Thompson 1996 Traeholt 1994).

Collecting field scats has also been used to examine the diet of varanids (Gaulke 1991; Traeholt 1994; Weavers 1989). Owing to the completeness of digestion in the gut of varanids, scats can provide biased information on ingested diet. Despite this, several authors have found scats to provide useful additional information on diet (Gaulke 1991; Traeholt 1994; Weavers 1989). This study will also include an examination of *V. mertensi* scats. A subsidiary aim of this chapter was to assess the difference between analysing stomach and scat contents samples to determine the diet of *V. mertensi*.

4.3 Aims

The specific aims of this chapter were to;

(1) describe the diet of *V. mertensi* in the ORIS and EK/VRD bioregion;

(2) examine geographical and seasonal variation in the diet of *V. mertensi*;

(3) describe the foraging behaviour of *V. mertensi*; and

(4) assess the difference between analysing stomach and scat contents to determine the diet of *V. mertensi*.

4.4 Materials and methods

To compile data on diet, flushed stomach contents, dissection of stomachs collected from dead specimens, field scat collection and feeding observations were used. Estimates of the abundance of the most common prey, *Holthuisana* sp. (freshwater crabs), were also made to determine if seasonal differences in the availability of crabs influenced the diet of *V. mertensi*. Foraging behaviour was observed during both day-to-day field activities and during continuous observation days of active radio-tagged individuals (Chapter 2). An indication of how often *V. mertensi* fed was obtained by comparing the proportion of empty and full stomachs sampled.

4.4.1 Stomach flush samples

Field-captured *V. mertensi* were stomach-flushed using the methods described by Legler (1979). Individuals were restrained and a plastic tube (approximately 1 cm in diameter and 1 m in length) was inserted down the esophagus past the glottis until the distal end of the stomach was reached. To ensure insertion into the stomach, progress of the tube down the esophagus and stomach, was felt through the abdominal wall. A large hand pump (a modified air mattress pump) was used to pump approximately 500-600 ml of water through the tube into the stomach. Stomach contents flushed from individuals were collected in a colander (sieve size 2 mm). Water was pumped into each individual 3 to 6 times before the plastic tubing was removed. Extraction of the tubing while water was being pumped proved most successful in extracting larger stomach contents as such items often became stuck behind the tubing during flushing. Large items were usually regurgitated upon removal of the tubing. Stomach contents were stored in 70% ethanol.

Stored stomach contents were later dried for a period of 7 days at 35 ºC before being sorted into prey constituent groups under a dissecting microscope. To ensure that all excess water was removed from samples, a sub-set of five of the largest samples (based on volume) was weighed repeatedly through the drying process. Samples were only considered devoid of moisture when their mass remained constant for three successive days. Prey groups were weighed to record the dry mass of each constituent prey group in each stomach content sample. The minimum

number of individual prey items in each stomach was also counted. This involved counting diagnostic portions of prey items found in each prey group. For example, for freshwater crabs (*Holthuisana* sp.), the number of claws divided by two was taken as indicative of the number of crabs ingested.

4.4.2 Stomachs from dead animals

Stomach content samples were also collected from dead animals encountered opportunistically during the field study. The majority of these animals were recovered from the roadside after being killed by traffic. The stomachs of individuals were opened, their contents removed and stored in 70% ethanol to be later dried and sorted in a similar fashion to stomach samples obtained through flushing.

4.4.3 Scat samples

Scats were only collected from deposit sites within close proximity to waterbodies known to be frequented by *V. mertensi*. To distinguish scats left by *V. mertensi* from those of other species, such as water birds, *V. mertensi* were first observed defecating and their scats collected. Scats of several individuals were collected and closely examined to identify their form and constituents. Scats were cylindrical with dimensions approximately 100 mm by 10 mm. Scats often contained large solidified globules of uric acid. Scats matching this description were collected and stored in 70% ethanol. Following drying, for a period of 7 days at 35 ºC, scats were also sorted and the dry mass of all constituent prey groups within each scat was recorded along with the minimum numbers of prey items in each group.

4.4.4 Foraging observations

Numerous observations of foraging behaviour and prey capture were recorded during the field study. Observations were made both opportunistically during field activities, and during continuous observation days of active radio-tagged individuals (see Chapter 2 for details). All observations of *V. mertensi* foraging, detecting, pursuing, capturing and consuming prey were recorded and used to describe the foraging behaviour of *V. mertensi*. Both terrestrial and aquatic foraging behaviour was described based on these observations. Additionally, prey items observed being consumed by *V. mertensi* during these observations were recorded and added to dietary data.

4.4.5 Seasonal differences in the availability of *Holthuisana* sp.

The most predominant prey item consumed by *V. mertensi* in the East Kimberley was *Holthuisana* sp. (freshwater crabs). Estimates of the relative abundance of these freshwater crabs were undertaken during the late dry season in 2002 and the beginning of the wet season in 2003. It was envisaged this would indicate any seasonal differences in the availability of crabs and would provide insight into seasonal differences in the diet of *V. mertensi*. Additionally, estimates would give an indication of the importance of crabs as a prey source to *V. mertensi* residing in irrigation channels. Measurements of crab availability took place at a site on the Main Irrigation Channel (IPM1) of the Ivanhoe Plains Irrigation Area approximately 10 km north of the Kununurra townsite. This site was selected as it provided easy access to banks that contained numerous burrows made by crabs. The site was marked and the same location used for both wet and dry season estimates. Availability was estimated by counting the number of active burrows on three 3-5 m sections of the bank for three consecutive days. Initially, the surface of the bank was raked clear of any excavated mud at the entrance of each burrow. An active burrow was defined by a small pile of excavated mud at the entrance to a burrow in the morning. This indicated crab activity within that burrow during the night. The proportion of active and non-active burrows was determined as was the number of active burrows m^2 of irrigation channel bank. It was anticipated this would give an indication of the availability of crabs to a foraging *V. mertensi* probing burrows along such a bank.

4.5 Results

4.5.1 Diet of *V. mertensi*

The contents of 42 stomach samples and 25 scat samples from *V. mertensi* are summarised in Appendix 4.1. Samples were collected at various times during 2001, 2002 and 2003. Sixteen different prey groups were identified in stomach and scat samples; of these, six were insects, two were crustaceans and five were vertebrates. The remaining three prey groups were Arachnida, fruit and carrion.

Examining the number of items in each prey group allowed for a comparison of the relative abundance of each prey group. This combined with data on the number of varanids known to have consumed each prey group provided an indication

of how often and in what numbers each prey group was consumed. Freshwater crabs *Holthuisana* sp. were the most predominant prey item consumed by *V. mertensi*, with 45 (32.6%) and 91 (70.9%) recovered from stomachs and scats respectively. Nineteen stomachs and 17 scats contained crabs. Fish were the second most predominant prey group in stomachs but were absent from scats. Nineteen fish (13.7%) were recovered from stomachs of six individuals.

Reptile eggs represented a large proportion of the remaining prey items (31.1% and 9.4% of dry biomass recovered from stomachs and scats respectively, and 7.9% and 7.8% of all prey items recovered from stomachs and scat respectively). Eggs were found in 4.7% of the stomachs and 12% of the scats. These results suggest that eggs were rarely consumed, but when consumed constituted a large proportion of diet biomass. Frogs, similar to eggs, appear to be only rarely consumed but constituted a large proportion of diet biomass (Appendix 4.1). In contrast, spiders were consumed frequently but only represented a small proportion of biomass consumed (Appendix 4.1). Water bugs and black beetles, like spiders, were consumed frequently but only represented a small proportion of biomass consumed (Appendix 4.1). The only other prey group representing greater than 5% of either total prey items recovered or biomass was mice (0.7% of prey items recovered and 8.1% of dry biomass). Prey groups such as crickets, grasshoppers, unidentified insects, unidentified insect larvae (caterpillars), reptiles (Agamidae), carrion, fruit and red claw (*Cherax quadricaratinus*) each represented less than 5% of the number of prey items recovered or total biomass recovered.

4.5.2 Stomach contents and scat samples

Significantly fewer soft-bodied prey items were recovered from scats compared to stomachs ($\chi_1^2 = 44.764$, $P < 0.0001$) (Appendix 4.1). In particular, freshwater crabs comprised 70.9% of total prey number and 83.7% of total biomass in scats compared to 32.6% of total prey number and 29% of total biomass in stomachs (Appendix 4.1). Prey groups absent from scat samples included spiders, crickets, caterpillars, fish, frogs, reptiles, carrion and fruit (Appendix 4.1). An additional prey group in the diet of *V. mertensi* identified in one field scat sample was the decapod, red claw or *Cherax quadricaratinus*, which comprised 0.8% of prey items and 1.7% of biomass. This is the first recording of red claw being

consumed by *V. mertensi* and is interesting given that red claw have only recently been introduced into waterways of the Ord River (Doube *et al.* 2004).

Despite scats proving informative, no scat data were included in the following examination of seasonal differences in diet as the deposit date of scats could not be established. Dietary data from scats were used to gain an indication of variation in the diet of *V. mertensi* at natural and human-altered watercourses of the East Kimberley. This was done as stomach content data for comparison was limited. However, when examining diet based on scats, any results should be viewed cautiously due to the absence of soft-bodied prey groups from scats and hence a sample bias.

4.5.3 Variation in the diet of *V. mertensi* in the East Kimberley

The contents of 17 scats collected at human-altered watercourses of the ORIS and seven from natural watercourses are show in Figure 4.1. As only seven scats were collected from natural watercourses no statistical analysis was undertaken. Despite a lack of statistical analysis some trends are apparent. A higher proportion of freshwater crabs were found in scats collected at natural watercourses than at human-altered watercourses (Figure 4.1). Black beetles also comprised a higher proportion of scats collected at natural watercourses (Figure 4.1). Interestingly, eggs were only found in scats collected at human-altered watercourses, as were grasshoppers, mice and red claw.

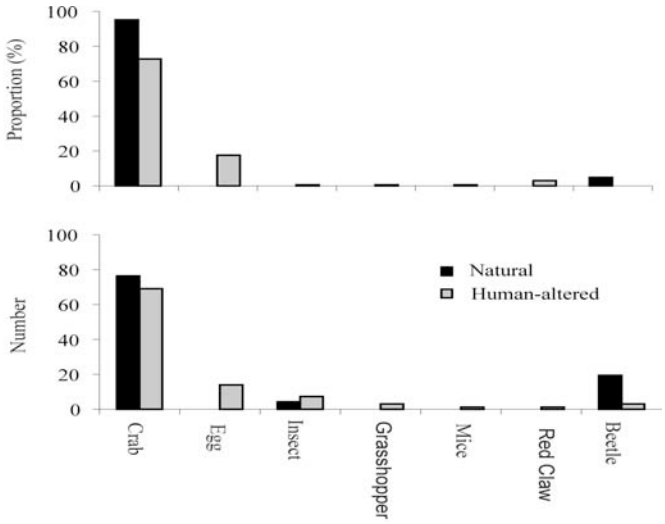


Figure 4.1: Proportion of total biomass and the number of prey items recovered from *V. mertensi* scats collected at natural and human-altered watercourses of the East Kimberley.

Unfortunately stomach content data obtained for both seasons during the study were insufficient to allow statistical analysis of seasonal differences in diet. The contents of seven stomachs were collected during the dry season while 33 stomach contents were collected during the wet season. Such a low sample size for dry season months resulted from a reduced number of *V. mertensi* being active during dry season months (Chapter 6). Despite a lack of statistical analysis, again some trends are apparent and are discussed in the following paragraphs.

A total of five different prey groups were consumed during dry season months while 15 were consumed during wet season months (Figure 4.2). Crabs represented both a larger proportion of prey biomass and total number of prey items during the wet season when compared with the dry season (Figure 4.2). Two out of 7 stomachs (28.6%) sampled during the dry and 16 out of 33 (48.5%) sampled during the wet season contained crabs. Unfortunately low sample size again rendered a Chi-squared analysis of these data inappropriate (expected values < 5). Fish, spiders and insects comprised both a larger proportion of biomass and total prey number in the dry compared to wet season.

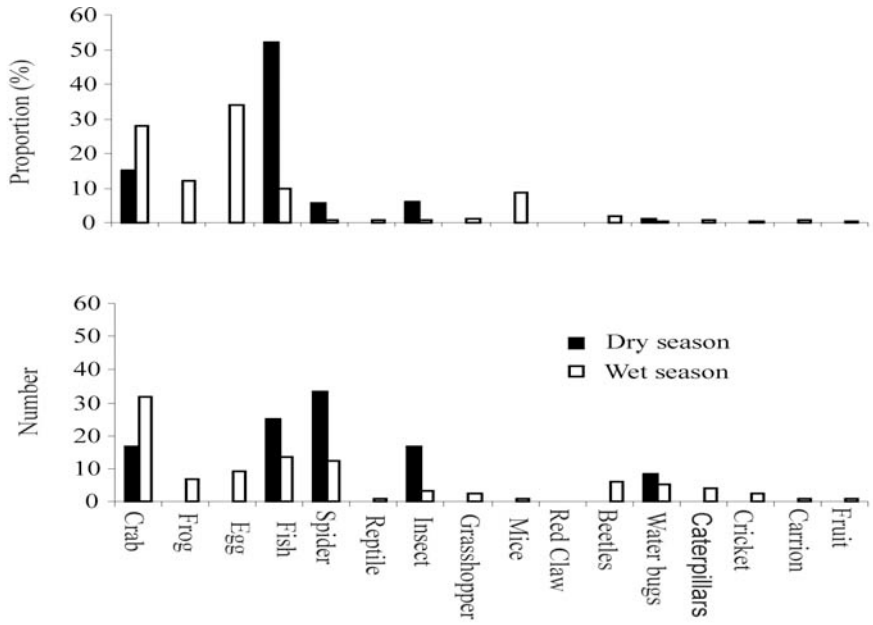


Figure 4.2: Proportion of the total stomach contents biomass represented by each prey group and the total number of prey items found in stomach contents belonging to each prey group. Dry season data includes all samples taken between 1st of April and 1st of November in the years 2001 - 2003 (n = 7) and wet season data includes all samples taken between 1st of November and 1st of April in the years 2001 - 2003 (n = 33).

4.5.4 Seasonal variation in prey availability

Freshwater crabs (*Holthuisana* sp.) made up a larger proportion of stomach contents during the wet compared to dry season (Figure 4.2). More than twice as many crab burrows were present in the irrigation channel bank during the dry compared to the wet season (Table 4.1). The proportion of crab burrows actively used during the wet season (27.7%) was, however, higher compared to the dry season (21.3%). This suggests that a foraging *V. mertensi* probing burrows to locate crabs would need to probe more burrows during the dry than during the wet season to locate crabs.

Table 4.1: The number of active crab (*Holthuisana* sp.) burrows during the late dry season of 2002 and early wet season of 2003

Season	Total # burrows	Total # active burrows	% active
Wet			
Day 1	32	8	25
Day 2	23	5	21
Day 3	28	10	35
Total	83	23	
Mean	**27.67**	**7.67**	**27.71**
Dry			
Day 1	77	16	20
Day 2	44	11	25
Day 3	48	9	18
	169	36	
Mean	**56.33**	**12.00**	**21.30**

Fish also represented a larger proportion of the diet during the dry compared to wet season (Figure 4.2). Over the course of the study an herbicide (Acrolein/Magnicide, 2-Propenal, Magna Herbicide Division Baker Performance Chemicals Inc) was observed being frequently injected into irrigation channels by the water regulatory authority "Ord River Irrigation Co-operative". Herbicide injections were used to control the growth of water plants that prevent efficient water flow through irrigation channels (pers. comm, Bruce Carwadine, 2001). These injections kill water plants and most gilled organisms residing within irrigation channels. Large-scale fish deaths occurred 1-2 days after these injections of herbicide

providing an easily obtainable prey resource for *V. mertensi*. Dead freshwater crabs (*Holthuisana* sp.) were never observed after the injection of herbicide.

Fish were recorded in the stomachs of *V. mertensi* captured in irrigation areas on the following dates; 11/1/01 (n = 1), 16/1/01 (n = 2), 11/5/01 (n = 1) and 22/3/02 (n = 1). In four out of five cases (80 %) these dates coincided with Acrolein/Magnicide injections (Table 4.2).

Table 4.2: The location, date and season of herbicide (Acrolein/Magnicide) injections into irrigation channels during the years 2001 - 2003. Total number of herbicide injections undertaken during each season also shown. * denotes injections that coincided with the capture of *V. mertensi* containing fish in their stomachs. ** denotes two such captures.

Date	Season	Sections treated	Evident kill
12/1/01**	Wet	Ivanhoe	Yes
24/4/01*	Dry	Ivanhoe	Yes
24/7/01	Dry	Ivanhoe	Yes
28/8/01	Dry	Ivanhoe	Yes
1/10/01	Dry	Ivanhoe	Yes
30/10/01*	Dry	Ivanhoe	Yes
9/4/02	Dry	Ivanhoe/Packsaddle	Yes
14/5/02	Dry	Ivanhoe/Packsaddle	Yes
25/6/02	Dry	Ivanhoe/Packsaddle	Yes
13/8/02	Dry	Ivanhoe	Yes
10/9/02	Dry	Ivanhoe/Packsaddle	Yes
15/10/02	Dry	Ivanhoe	Yes
5/11/02	Wet	Packsaddle	Yes
19/11/02	Wet	Ivanhoe	Yes
Total (Wet)	3 Events		
Total (Dry)	11 Events		

4.5.5 Prey groups identified through feeding observations

During the field study several feeding sequences were recorded. Several prey groups seen eaten were also found in stomach content or scat samples including frogs, fish, crabs, and grasshoppers. A legless lizard was not found in either stomach contents or scats but was seen being eaten. The legless lizard was consumed by a radio-tagged individual (# 17) during an observation day in 2002 in the Packsaddle Plains Irrigation Area. Several small eel-tail catfish, another prey group not identified in stomach or scat contents, were eaten by animal #5.14 at Salerno Gorge Main Pool

during the dry season of 2002. Although the actual underwater capture sequences were not observed the individual was seen to return to the surface of the water, orientate the struggling fish and consume them head first.

4.5.6 Foraging behaviour of *V. mertensi*

During the field study, numerous *V. mertensi* were observed foraging. The majority of these observations were made from the terrestrial environment. Despite this, some underwater foraging sequences were observed in clear shallow water. Nine such recorded observations chosen to best illustrate the foraging behaviour of *V. mertensi* are outlined in the following paragraphs.

Observation 1 - Main Irrigation Channel (M1) in the Ivanhoe Plains Irrigation Area during the wet season of 2003

An individual was observed foraging while swimming along the bottom of the channel at a depth of approximately 2.5 m, moving its head from side-to-side searching under rocks, tongue flicking approximately every 5 - 6 seconds. After investigating around the edge of three rocks the individual forced its head under the edge of a fourth rock 3 - 4 times, to a depth of approximately 10 - 15 cm while repeatedly tongue flicking. On the final attempt a small freshwater crab (*Holthuisana* sp.) shot out from under the rock and swam up through the water column. The crab had gained about 1.5 – 2 m on the lizard before the lizard retracted its head from under the rock, and chased and caught the crab before returning to the surface. By this time the individual had been underwater for several minutes. After 2 - 3 attempts to orientate the crab, the individual swallowed it without any apparent chewing whilst swimming against an obvious current on the surface of the water. The individual then returned to the bottom of the channel and continued its underwater foraging.

Observation 2 – Irrigation channel drain (D4) in the Ivanhoe Plains Irrigation Area during the late wet season of 2002

An individual was observed standing on the edge of an artificial waterfall, snatching fish out of the air as they attempted to jump up through the waterfall. This *V. mertensi* was seen to catch three fish. After each successful capture the individual would leave the waterfall and retreat approximately 5 m into the hinterland before

orientating the fish head first in its mouth and swallowing it. Swallowing usually required 2 - 3 attempts and in one instance the fish was dropped onto the ground where it was quickly retrieved before it was able to return to the water, and swallowed. Two fish were small *Leiopotherapon macrolepsis* (Kimberley Spangled Perch) and the other was a small *Amniataba percoides* (Stripy). Following consumption of these three fish, the individual left the waterfall and began foraging along the edge of the irrigation channel, walking slowly along the bank moving its head from side-to-side searching the riparian vegetation with regular tongue flicking.

Observation 3 - Main Irrigation Channel (M1) in the Ivanhoe Plains Irrigation Area during wet season 2002

An individual was observed probing numerous freshwater crab burrows, repeatedly tongue flicking when moving between burrows, on the bank of an almost completely drained main irrigation channel. After probing three burrows, to a depth of 15 - 30 cm, the individual retracted its head from a fourth burrow with a freshwater crab (*Holthuisana* sp.) in its mouth. It immediately arched its head back and swallowed the crab without any apparent orientation of the prey. After swallowing the crab this individual sighted the observer and walked off, discontinuing its foraging.

Observation 4 - Main Irrigation Channel (M1) in the Ivanhoe Plains Irrigation Area during the dry season of 2002

An individual was observed slowly walking through vegetation along the bank of the irrigation channel moving its head from side-to-side and regularly flicking its tongue. After no visible pursuit the individual was seen grasping an unidentified frog in its mouth. It arched its head back and orientated the frog head first before struggling momentarily to swallow the frog. After a further period of 30 - 60 sec of foraging amongst vegetation in which the first frog was captured the individual was seen grasping a second frog in its mouth, which it swallowed in the same fashion as the first.

Observation 5 - Packsaddle Plains main irrigation channel during an Acrolein injection in the dry season of 2002

After approximately 2 - 3 minutes of watching dead fish float past (as a consequence of an Acrolein/Magnicide injection into the channel) a *V. mertensi* was observed to swim out into the channel to capture a fish that was obviously distressed but not dead. This individual returned to the bank and consumed the fish head first, before returning to the observation point on the bank. It remained stationary on the bank basking for a further 10 minutes before being disturbed by a passing vehicle and leaving the area.

Observation 6 - Packsaddle Plains main irrigation channel during the dry season of 2002

An individual was first observed slowly foraging along the bank/water interface, moving its head from side-to-side and regularly tongue flicking, when its attention was attracted to the nearby riparian zone. After leaving the water, the individual quickly pursued and caught a jumping grasshopper within the riparian vegetation. After consumption, which involved no apparent orientation of the insect, the individual returned to water/bank interface and resumed its slow moving, foraging behaviour along the interface.

Observation 7 - Packsaddle Plains main irrigation channel during the dry season of 2002

An individual was observed slowly moving along the bank/water interface of the irrigation channel, moving its head from side-to-side and regularly tongue flicking. The lizard's attention was suddenly drawn to the nearby fringing vegetation and it promptly left the bank/water interface to investigate. Suddenly, the lizard began to pursue an unknown prey item in this vegetation. After an unobserved pursuit of approximately 3 - 4 m the animal raised its head to swallow a legless lizard (Pygopodidae) approximately 30 cm in total length. After consuming the legless lizard the individual resumed searching the same fringing riparian vegetation for a further 1 - 2 minutes before returning to the water where it resumed its slowly moving foraging behaviour.

Observation 8 - Natural waterhole at Salerno Gorge on El Questro Station during the late dry season of 2002

An individual actively chased and caught two small live eel-tail catfish (*Neosilurus* sp.) in the main pool. Although not sighted during the actual capture sequence, due to the depth of water, the individual returned to the surface with these fish still struggling in its mouth. The animal proceeded to consume both fish while swimming on the surface of the water after carefully orientating them into a head first position.

Observation 9

Although not a direct observation of *V. mertensi* pursuing, capturing and consuming prey several anecdotal instances noted during the field study warrant recording. These involved *V. mertensi* being repeatedly captured in enclosed nets used to capture freshwater crustaceans by fishers throughout the Ord River and surrounding areas. Three such instances were observed during the course of field work all resulting in the unintentional death of *V. mertensi* captured in such traps. Traps used were enclosed "Opera House" cage traps available from any fishing tackle supplier and were baited in all instances with meat scraps and submerged in approximately 5 meters of water. Dead animals were found drowned in traps by fishers upon checking traps to retrieve their catch. In all instances trap baits were not taken although traps were devoid of any fish or crustaceans. This suggests that trapped *V. mertensi* may have entered traps not for the carrion bait but for trapped fish or crustaceans already trapped within. The stomach contents of one drowned animal recovered from a natural waterhole on the Four Mile Creek system located approximately 30 km East of Kununurra (UTM: 52, 492163: 8243068) contained two fish of unknown identity.

4.5.7 Contents of stomachs

Sixty stomach content samples were collected during the field study and examined. This included a total of four stomachs recovered from deceased *V. mertensi* and 56 obtained through stomach flushing live specimens. Of these 60 samples, 42 (70%) contained one or more prey items. The frequency of stomachs containing more than one prey item was not significantly different between seasons (χ_1^2 = 0.627, P = 0.429). Seven out of 17 (41%) stomachs contained at least one

prey item during the dry season. Thirty three out of 54 (61%) stomachs contained at least one prey item during the wet season.

4.6 Discussion

4.6.1 Diet

Varanus mertensi in the East Kimberley and Northern Territory (Shine 1986) eat a diverse range of soft and hard-bodied items, most of which are found around the waters edge or in the water. There were minor differences in prey groups identified in the stomachs of *V. mertensi* in the East Kimberley and Northern Territory (Shine 1986). Prey groups not found in the East Kimberley diet included Hemiptera (bugs), Hymenoptera (ants), Brachyura (shrimps), Aves (birds), and Serpentes (snakes). Prey groups not reported by Shine (1986) but found in the East Kimberley diet included Decapoda (red claw), Nepoidea (water bugs), Agamidae (dragon lizards), caterpillars (unidentified larvae), carrion and fruit. These differences are probably an artifact of small sample sizes in both studies. These data suggest that *V. mertensi* is opportunistic, feeding on all available invertebrate and small vertebrate prey that it can catch and subdue in the aquatic areas it inhabits

This study and Shine (1986) indicate that freshwater crabs (*Holthuisana* sp.) are the predominant component of the diet of *V. mertensi*. The prevalence of freshwater crabs in the East Kimberley diet probably reflects prey availability rather than selective feeding. Availability of crabs along irrigation channel banks was as high as 1.7 ± 0.27 burrows m^{-2}. Given that individuals will forage up to 1 km along an irrigation channel during a day's activity (Chapter 6), crabs on channel banks present a significant potential prey resource. Angelici and Luiselli (1999) also reported that the diet of the semi-aquatic *V. niloticus* consisted mainly of locally abundant crabs found throughout the Niger Delta. Interestingly, fewer crabs were consumed by *V. mertensi* examined from the Western Australian Museum collection (Shine 1986) than for specimens examined in the East Kimberley (Appendix 4.1). This difference is probably due to the higher availability of freshwater crabs in areas where *V. mertensi* were captured in this study.

The majority of prey consumed by *V. mertensi* originates from either the aquatic or riparian zone. This is similar to reports of diet of other semi-aquatic varanids. For example, Shine (1986) reported that *V. mitchelli* feed predominately on fish in Northern Australia, *V. semiremex* feed predominately on crustaceans in

Northern Australia (Bustard 1970; James *et al.* 1992), *V. salvator* feed predominately on crustaceans in undisturbed areas of Malaysia (Gaulke 1989; Gaulke 1991; Losos and Greene 1988) and *V. niloticus* feed predominately on crabs in the Niger Delta and mollusks in Cameroon (Angelici and Luiselli 1999; Lohnberg, 1903).

The majority of prey items consumed were relatively small compared to the body size of an adult *V. mertensi*, with the four largest individual prey items consumed by *V. mertensi* (in decreasing size) being a mouse, small fish, crabs and reptile eggs. Although the individual wet mass of each prey item was not measured, it would appear that a large prey item, such as a mouse, weighing approximately 15 - 20 g, would only represent 0.6 % of the body mass of an average adult *V. mertensi* weighing 2 kg. This is a much smaller proportion than that reported for single dietary items of some other varanids. For example, *V. panoptes* have been reported to consume *V. gouldii* totalling 11 % of their body mass (Christian 1995), and an adult *V. varius* (weighing 20.4 kg) was reported to regurgitate four fox cubs, three small rabbits and three large blue-tongued lizards (Fleay 1950). *Varanus giganteus* is capable of consuming large vertebrate prey (King *et al.* 1989) such as possums (*Trichosurus arnhemensis*), bandicoots (*Isoodon auratus*) and young Euro's (*Macropus robustus*), and *V. komodoensis* have been reported to consume large vertebrate prey including domestic animals such as goats and pigs (Auffenberg 1981; 1994).

4.6.2 Variation in diet

Unfortunately data on seasonal variation in the diet of *V. mertensi* examined in the East Kimberley was limited preventing statistical analysis. Scats proportionally contained more black beetles and crabs at natural watercourse sites compared to human-altered waterbodies. This suggests that crabs and black beetles may be more available within natural waterbodies. Interestingly, less abundant prey groups such as eggs, grasshoppers, mice and red claw were only recovered from scats collected at human-altered waterbodies of the ORIS. With the exception of red claw, that was only recently introduced into the ORIS (Doube *et al.* 2004), these absences may reflect a low sample number at natural waterbodies. These trends, however, warrant further investigation. Future data collection in this area should only include dietary

data from stomach content samples rather than scats to avoid significant bias against soft-bodied prey items identified in this study.

To date, there has been no analysis of seasonal variation in the diet of *V. mertensi*. Unfortunately, due to both a lack of active *V. mertensi* available for opportunistic capture and individuals trapped not being stomach flushed, this study obtained little additional seasonal data. Further sampling, particularly during dry season months, might verify the trends suggested by this study that proportionally more *Holthuisana* sp. were consumed during the wet compared with the dry season. Proportionally more fish, spiders and insects were also consumed during the dry season. This suggests that crabs may not be as easily caught during the dry season by foraging *V. mertensi*. In support of this, estimates of crab availability showed less burrows contained a crab during the dry season. In contrast, fish, spiders and insects may be more easily obtained during the dry than the wet season. No supporting data on the relative abundance of these prey groups were recorded.

4.6.3 Techniques and sampling effort required to determine diet

Stomach content sampling provided a more comprehensive appreciation of the diet of *V. mertensi* than did scats. This is due to soft-bodied prey being more completely digested, and only hard indigestible prey fragments passing into scats. Despite this, scats were still a useful source of data given the ease of sampling, as collecting scats does not involve having to capture and handle animals. This suggests that scats should be collected in addition to stomach contents samples. This increases the number of individuals sampled and may identify additional hard-bodied prey groups not identified in stomach contents samples. For example, in this study an individual *Cherax quadricarinatus* (Red Claw) was identified in only one scat sample. In interpreting dietary data from scats, any analysis should consider the significant bias against soft-bodied prey groups in scat samples.

If future studies aim to stomach flush *V. mertensi* to examine diet, then the number of empty stomachs encountered in the field can now be anticipated based on the findings of this study. In this study, 61% of stomachs were found to contain at least one prey item during the wet season and 41% during the dry season. More samples should be collected during the dry season to account for this seasonal difference. Additionally, twice as many individuals should be stomach flushed as is

required to determine the diet of *V. mertensi* given that approximately 50% of stomachs will be empty upon flushing.

4.6.4 Foraging behaviour

The foraging behaviour of *V. mertensi* incorporates slow, forward movement with progressive swaying of the head from side-to-side and regular tongue flicking to detect the presence of prey. This search pattern, which is used both in the terrestrial and aquatic environments, has also been described for *V. gouldii* (Thompson 1995). The regular side-to-side movement of the head and flicking of the forked tongue presumably maximises the detection area for olfactory receptors (Jacobson organ) located on the roof of the mouth (Auffenberg 1983; Cooper 1989; Garrett and Card 1993). Data from this study suggests *V. mertensi* are capable of searching for and capturing prey underwater using olfactory cues. This has only previously been reported for the semi-aquatic *V. salvator* which has been reported as capable of foraging in fresh, brackish and saltwater (Gaulke 1989).

In addition to detecting prey using olfactory cues while foraging, *V. mertensi* also used their visual sense. Observations of *V. mertensi* pursuing and capturing grasshoppers, small lizards and fish suggests that their eyesight is acute. Likewise an observation of an individual capturing several live fish in a waterhole suggests that their eyesight is also acute underwater. Observations of a submerged individual flushing an unsighted crab from under a rock and another catching crabs in their burrows suggests that *V. mertensi* are equally adept at seeking out unsighted prey. In a similar manner, Thompson (1995) described how *V. gouldii* were able to locate mole crickets and spiders hidden in burrows based on olfactory cues. The use of both olfactory and visual cues to detect prey is common in terrestrial varanids (Christian 1995; Thompson 1995; Traeholt 1993) but *V. mertensi* seems to use these senses very effectively in an aquatic environment. A visual depiction of this underwater foraging ability can also been seen in a segment of a documentary (ABC Natural History Unit "From the Heart" series, 2003) further supporting the findings of this study.

Interestingly, *V. mertensi* were rarely observed pursuing and capturing healthy fish within the aquatic environment. Although I did observe *V. mertensi* on three occasions to catch fish, on only one occasion was an individual observed pursuing and capturing slow moving healthy eel-tail catfish (*Neosilurus* sp.) within

a waterhole. The other two observations were of fish that were either dying or had restricted movement (e.g. fish negotiating a waterfall or dying after herbicide injections). Hermes' (1981) observation of *V. mertensi* capturing fish confined within a small drying pool, when combined with the results of this study, indicates that *V. mertensi* are capable of adapting their foraging strategies to take advantage of the various ways in which potential prey present themselves.

Very few of a large number of dying fish washed down irrigation channels during herbicide injections were consumed by *V. mertensi.* Long-term decaying carrion baits used in treadle traps also failed to attract *V. mertensi* (pers. obs). These data suggest that *V. mertensi* will eat live fish when they can be caught, but are reluctant to eat decaying dead fish or carrion. In a captive situation or around areas of human activity (e.g. caravan parks, camping areas), *V. mertensi*, like other large varanids, will readily adapt to eating dead fish and cooked meat scraps (pers. obs). This is similar to the flexible diet of *V. salvator* described by Gaulke (1991) and Traeholt (1994) where individuals were reported to consume carrion left by tourists in populated areas.

All observations suggest that *V. mertensi* forage either in the water (usually along the benthos), along the bank/water interface or through riparian vegetation fringing waterbodies. The bank/water interface represents an area of high concentrations of active crab burrows along irrigation channels. *Varanus mertensi* foraging along this interface can search for freshwater crabs by probing burrows while simultaneously remaining vigilant for potential prey movement in nearby riparian vegetation. This aquatic foraging behaviour is reflected in the daily behaviour of *V. mertensi* which incorporates extensive aquatic activity (Chapter 3).

An observation of an individual successfully capturing numerous fish negotiating a waterfall combined with anecdotal evidence reporting similar foraging behaviour by other *V. mertensi* on separate occasions (pers. com. Paul Raftery, 2002) suggests individuals are capable of drawing on previous prey capture success to increase their foraging efficiency. This capacity to recall previous feeding experiences was also shown during feeding trials conducted on *V. salvator* (Traeholt 1993). Pianka *et al.* (2004) also provides a range of examples demonstrating the capacity of varanids to learn from prior experience.

Other than for a single example of *V. mertensi* using a “sit-and-wait” strategy to catch fish negotiating a waterfall, which I believe was atypical foraging

behaviour, *V. mertensi* are predominately active foragers and in this regard are similar to many other semi-aquatic and terrestrial varanids. However, several exceptions to this have been reported including *V. komodoensis* (Auffenberg 1972; 1978; 1981), *V. bengalensis* (Auffenberg 1983; 1994), *V. griseus* (Tsellarius *et al.* 1997) and *V. glebopalma* (Sweet 1998) that have been shown to display predominately "sit-and-wait" foraging behaviour.

Appendix 4.1: The diet of *V. mertensi* in the East Kimberley examined in stomach contents and scat sample collected during the years 2001 - 2003 compared to the diet of *V. mertensi* in the Northern Territory and Western Australia described by Shine (1986) using stomach contents samples obtained from museum specimens in Western Australia and field captured animals from the Northern Territory. ~ denotes prey group absent from sample and no = number of individuals.

	Northern Territory (Shine, 1986)			**Western Australia (Shine, 1986**			**Kimberley (Stomachs)**			**Kimberley (Scats)**		
Prey group	# prey	Mass(g)	no	# prey	Mass(g)	no	# prey	Mass(g)	no	# prey	Mass(g)	no
Arachnida							19(0.14)	0.693(0.01)	9	~	~	~
Lycosidae	4(0.03)	0.37	4	2(0.02)	0.2(0.002)	2	~	~	~	~	~	~
Unidentified Araneae	1(0.007)	0.13	1	~	~	~	~	~	~	~	~	~
Hexapoda												
Odonata	1(0.007)	0.3	1	4(0.04)	1.4(0.014)	2	~	~	~	~	~	~
Orthoptera	3(0.02)	0.64(0.001)	3	4(0.04)	2.65(0.03)	4	~	~	~	~	~	~
Grylidae (crickets)	1(0.001)	0.3	1	2(0.02)	1(0.01)	1	3(0.022)	0.1841(0.003)	2	~	~	~
Acrididae (grasshoppers)	~	~	~	1(0.01)	1(0.01)	1	3(0.022)	0.6266(0.01)	3	2(0.02)	0.41(0.003)	1
Gryllotalpidae (mole crickets)	1(0.007)	0.5	1	~	~	~	~	~	~	~	~	~
Hemiptera	1(0.007)		1	20(0.20)	2.30(0.02)	3	~	~	~	12(0.1)	2.5(0.02)	5
Nepidae	3(0.02)	1.55(0.002)	1	2(0.020)	1.25(0.01)	2	~	~	~	~	~	~
Nepiodea	~	~	~	~	~	~	7(0.051)	0.1905(0.003)	4	1(0.01)	0.022(0.0001)	1
Coleoptera	~	~	~	3(0.03)	4.8(0.048)	3	~	~	~	~	~	~
Dytiscidae	24(0.17)	9.05(0.013)	2	9(0.09)	6.4(0.064)	5	~	~	~	~	~	~
Carabidae	1(0.007)	~	1	~	~	~	8(0.058)	1.3449(0.02)	5	12(0.1)	2.5(0.02)	5
Hymenoptera												
Formicidae	1(0.007)	0.08	1	~	~	~	~	~	~	~	~	~
Unidentified insects	2(0.014)	~	~	6(0.061)	0.4(0.004)	2	6(0.043)	0.6039(0.01)	5	7(0.05)	0.62(0.004)	4
Insect larvae	~	~	~	~	~	~	5(0.036)	0.5144(0.008)	4	~	~	~
Holthuisana	69(0.49)	205.6(0.29)	21	3(0.03)	14(0.14)	3	45(0.33)	19.28(0.29)	19	91(0.71)	112.52(0.84)	17
Decapoda	~	~	~	~	~	~	~	~	~	1(0.008)	2.27(0.017)	1
Caridae (shrimps)	10(0.07)	5.07(0.04)	1	19(0.19)	10.8(0.11)	3	~	~	~	~	~	~
Pisces	4(0.03)	1.4(0.002)	3	5(0.05)	29.9(0.3)	4	19(0.137)	7.61(0.115)	6	~	~	~
Anura	5(0.036)	30.7(0.043)	4	5(0.05)	3.0(0.03)	3	8(0.06)	7.39(0.11)	3	~	~	~
Reptile(eggs)	6(0.043)	420(0.594)	1	2(0.02)	20(0.20)	1	11(0.079)	20.68(0.31)	2	10(0.08)	12.64(0.1)	3
Serpentes	1(0.001)	30(0.042)	1	~	~	~	~	~	~	~	~	~
Agamidae	~	~	~	~	~	~	1(0.007)	0.359(0.005)	1	~	~	~
Aves	1(0.001)	~	1	1(0.01)	~	1	~	~	~	~	~	~
Mammalia	1(0.001)	1.8(0.003)	1	1(0.01)	~	1	~	~	~	~	~	~
Mus musculus (house mouse)	~	~	~	~	~	~	1(0.007)	5.355(0.08)	1	1(0.008)	0.302(0.002)	1
Carrion	~	~	~	~	~	1	1(0.007)	0.439(0.006)	1	~	~	~
Fruit	~	~	~	~	~	1	1(0.007)	0.218(0.003)	1	~	~	~
Other	~	~	~	~	~	~	(0.047)	0.9022(0.014)	7	~(0.3)	3.21(0.024)	8
Totals	**140**	**707.49(1)**	**31**	**99**	**99.65**	**34**	**138(1)**	**66.39(1)**	**42**	**128(1)**	**134.5(1)**	**25**

-Chapter 5-

Reproductive seasonality of *V. mertensi*

Publications resulting from this chapter

Mayes, P.J, Bradshaw, S.D and Bradshaw F.J (2005). Successfully determining the sex of adult *Varanus mertensi* (Reptilia: Varanidae) using a combination of both hemipenile eversion and the ratio of androgens:oestradiol in blood plasma. *Annals of the New York Academy of Sciences.* 1040: 402-406

Mayes, P.J, Bradshaw, S.D and Bradshaw F.J (In Press). The seasonal reproductive cycle of the semi-aquatic monitor *Varanus mertensi* (Reptilia: Varanidae). *Mertensiella*.

5.1 Summary

A previous study examining museum specimens of *V. mertensi* for gonadal development found reproductively active females during the wet season months of December – March (Shine 1986). This study adds to these data, reporting on both the reproductive cycle of female and male *V. mertensi*. High levels of male reproductive steroids suggest that spermatogenesis begins during the dry season months of July, August and September. This is supported by increased testicular volume and histological examination of the stages of spermatogenesis in museum specimens. However, mating was only observed between December and February. Females showed raised levels of reproductive steroid between December and February suggesting vitellogenesis occurs during these wet season months. This was supported by both field observations of egg-carrying females and museum records of gravid females during this period.

All data suggest that male *V. mertensi* exhibit a “disassociated breeding tactic” (*sensu* Crews), whereby males undergo spermatogenesis during the late dry season in preparation for breeding during the peak wet season up to 5 months later. In contrast, females exhibit an “associated breeding tactic” undergoing vitellogenesis and mating during peak wet season months. A similar disassociated male breeding tactic has been identified in the seasonally inactive *V. griseus koniecznyi,* (Auffenberg *et al.* 1990) and *V. griseus* (Vernet 1977) suggesting seasonal inactivity may influence the breeding tactics of male varanids.

5.2 Introduction

Reproductive efforts can have effects on a species ecology and behaviour. For example, the onset of the mating season can affect the movements of males as they move extensively in search of reproductively receptive females. As the overall aim of this study was to examine the ecology and behaviour of *V. mertensi* in waterbodies of the ORIS and surrounding East Kimberley, an understanding of reproduction by *V. mertensi* in these areas is required.

5.2.1 Reproduction in temperate, arid sub-tropical and tropical varanids

Most temperate zone varanids are vernal breeders, with only a few exceptions. Both males and females prepare for mating during the late winter to early spring (Carter 1999; King and Rhodes 1982), followed by mating in late spring (Carter 1999) with egg development and deposition during summer (Carter 1999; Green *et al.* 1999). Most arid sub-tropical varanids also have similar reproductive seasons, preparing for mating in spring (James 1996; James *et al.* 1992) and depositing eggs during the summer (James 1996; Thompson and Pianka 1999). James *et al.* (1992) suggested that temperate and arid sub-tropical varanids, although having similar reproductive seasons associated with summer, may vary their reproductive season slightly according to local temperatures. Thompson and Pianka (1999) also found that *V. tristis* vary the onset of their reproductive season with changes in local temperatures.

Tropical varanids, in contrast have various seasonal reproductive strategies (Cisse 1971). For example, dry-season egg-layers *V. timorensis* (King 1993), *V. mertensi* and *V. mitchelli* (Shine 1986), *V. spenceri* (Pengilley 1981), *V. glauerti* and *V. glebopalma* (James *et al.* 1992; Sweet 1999), deposit their eggs during dry season months. Others deposit eggs during the wet season months e.g. *V. panoptes* and *V. gouldii* (Shine 1986), *V. storri* (James *et al.* 1992), *V. semiremex* (James *et al.* 1992) and *V. kingorum* (James *et al.* 1992). Several explanations have been proposed for these interspecific differences in the reproductive seasons of tropical varanids. Firstly, reproduction may be timed to provide emerging hatchlings with a period of maximum prey availability (James *et al.* 1992; Wikramanayake and Dryden 1988). Secondly it may avoid the possibility of nest flooding (Shine 1986). Thirdly, females may invest in production of offspring after accumulating body condition during periods of high prey abundances (James and Shine 1985). Finally, the timing of egg-

laying may facilitate suitable incubation temperatures for development of eggs (James and Shine 1985). Despite interspecific differences, most male and female tropical varanids prepare synchronously for mating. A synchronous or associated breeding tactic has been suggested for *V. flavescens* (Auffenberg *et al.* 1989), *V. timorensis* (King 1993), *V. glauerti*, *V. glebopalma*, *V. storri*, *V. semiremex*, *V. kingorum* (James *et al.* 1992), *V. acanthurus* (King and Rhodes 1982), *V. varius* (Carter 1999), *V. tristis* (Thompson and Pianka 1999) and *V. brevicauda* (James 1996). To determine the seasonal onset of mating preparation for both male and female *V. mertensi* was one objective of this chapter.

5.2.2 Annual reproductive cycle of *V. mertensi*

The annual reproductive cycle of female *V. mertensi* inhabiting tropical northern Australia was described from museum specimens held by both the Western Australian and Northern Territory Museums (Shine 1986). Shine (1986) found females were vitellogenic in December, January, February and March, and two were gravid in April and one in June. He also found a heavily gravid female presumably ready to deposit eggs in mid December. Shine (1986) concluded that *V. mertensi* mate during the wet season, most probably during the months of December – February, and deposit their eggs during the early dry season. No data have been presented on preparation for mating by male *V. mertensi*.

To determine the seasonal reproductive cycle of *V. mertensi* levels of sex hormones in plasma, collected from field captured adult male and females, were measured. Specifically this study aimed to identify periods of elevated levels of androgens (An) in males and oestradiol (E_2) in females as indicative of the onset of sperm production and vitellogenesis respectively. Previous studies of other varanids have shown androgens stimulate spermatogenesis in male varanids (Jacob and Ramaswami 1975). Phillips and Millar (1996) also associated elevated levels of An and E_2 with periods of reproductive activity in male and female *V. albigularis*. Measurements of An and E_2 in the blood plasma of *V. mertensi* would thus seem appropriate to gauge their onset of reproductive activity.

Plasma samples collected throughout the two years of the field study were combined to give a 12-month picture of hormone levels for each sex. Observations of mating attempts, the presence of gravid females, and the emergence of hatchlings were also recorded during the field study. Additionally, *V. mertensi* specimens held

by both the Western Australian and Northern Territory Museums were examined. Testes of males and ovaries of females were measured to determine annual cycles of gonadal development. Testes biopsies were taken and examined histologically to determine spermatogenic cycle. All data were combined to give the most comprehensive examination of the seasonal reproductive cycle of *V. mertensi* as possible.

To determine sex hormone levels in plasma for each sex, the sex of sampled individuals must be known. A field technique commonly used to determine the sex of a wide range of reptiles, including varanids, is eversion of a male's hemipenes (Carter 1999; Fyfe *et al.* 1999). Laparoscopy and X-Ray examinations for hemipenes have also been used to identify male varanids (Card and Mehaffey 1994; Carter 1999; Schildger *et al.* 1999). However, recent identification of a hemiclitoris structure in varanids (Böhme 1995) has cast doubt on using hemipenile presence to unequivocally identify male varanids. Logistical constraints, imposed by conducting field work in such a remote locality, meant techniques requiring specialised equipment could not be used in this field study. This study presents a new method for determining the sex of field captured *V. mertensi* using a combination of traditional hemipenile eversion and levels of sex hormones in blood plasma samples.

5.3 Aims

The specific aims of this chapter were to:

(1) determine when females undergo vitellogenesis;
(2) determine when males produce sperm in their testes;
(3) determine the mating season of *V. mertensi*;
(4) determine when females lay eggs; and
(5) determine when hatchlings emerge.

5.4 Materials and methods

5.4.1 Collection of plasma

A total of 64 plasma samples were collected from adult *V. mertensi* (SVL > 370 mm). Sampling was concentrated on adults so as to minimise hormonal analysis on reproductively-immature individuals. Between 3-5 ml of blood was taken from the caudal vein using a 19 gauge needle and collected into a heparinised plastic centrifuge tube. Blood samples were refrigerated at 4 ^{o}C prior to being centrifuged

for 7 minutes at 4500 rpm to separate cells from plasma. Plasma was stored at -12 ^{o}C until hormonal analysis.

5.4.2 Determining the sex of sampled *V. mertensi*

Eversion of the male hemipenes was attempted on all sampled adult *V. mertensi*. Maximum pressure was applied with both thumbs to the ventral post-cloacal area on both sides of the tail. If hemipenes were everted on applying pressure an individual's *field sex* was recorded as male (♂), if no eversion took place after applying what was deemed adequate pressure, an individual's *field sex* was recorded as female (♀). If extensive tail musculature prevented adequate pressure (that known to be required to evert hemipenes in other males) being applied to evert the hemipenes, an individual's *field sex* was recorded as unknown (0). Simultaneously, blood samples were collected from individuals and assayed to determine An and E_2 levels using the methods described in following sections. Finally, a ratio of An:E_2 was calculated for each individual sampled based on measured hormone levels. The final sex of all *V. mertensi* sampled was determined using a combination of both hemipenile eversion and the ratio of An:E_2 measured in blood plasma.

5.4.3 Morphometric measurements

Snout-vent length (SVL), tail length (TL) and body mass (BM) were recorded for all sampled adults. Gravid or egg-carrying females were determined through palpation of the abdomen and noted. Before release, sampled animals were individually marked to enable future identification if recaptured (see Chapter 2 for details).

5.4.4 Measurement and histology of male testes

The testes of fourteen adult *V. mertensi* (SVL > 370 mm) from collections of the Western Australian and Northern Territory Museums, were measured. Overall length and maximum width of both testes were measured with Vernier calipers and the volume of each calculated based on the volume of an oblate spheroid. Testicular volume was plotted against month, regardless of the year of collection. Small biopsies were removed from the testes and transferred to Bouins solution to be routinely processed for paraffin sectioning. Sections of 6 µm were cut, stained with haematoxylin and eosin, and examined under both low and high power. Ten fields of

view were examined under 400x magnification using a light microscope. Spermatogenic activity in testes was scored as one of four categories; (1) *quiesescent* (Plate 5.1), indicated by only primary spermatogonia present in the wall of the tubule, (2) *recrudescent* (Plate 5.2), indicated by the presence of primary and secondary spermatocytes, (3) *sperm bundles* (Plate 5.3) and (4) *free sperm* (Plate 5.3), indicating the presence of free sperm within the seminiferous tubule.

Ovaries of females held in both museum collections were also examined. The diameter of any yolk-bearing follicles was measured and the volume calculated based on either the volume of a sphere (spherical follicles) or an oblate spheroid (oblate spherical follicles).

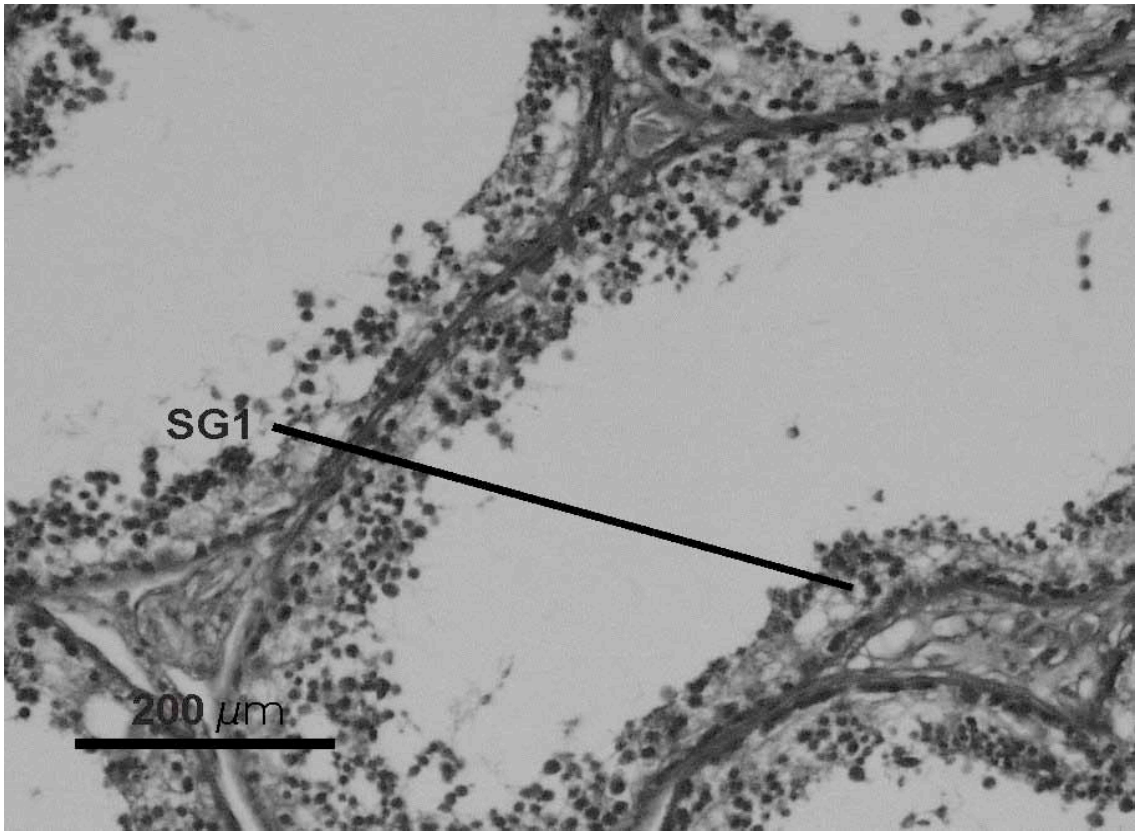


Plate 5.1: Quiesescent *V. mertensi* testis showing only primary spermatogonia cells (SG1) in the wall of the seminferous tubule.

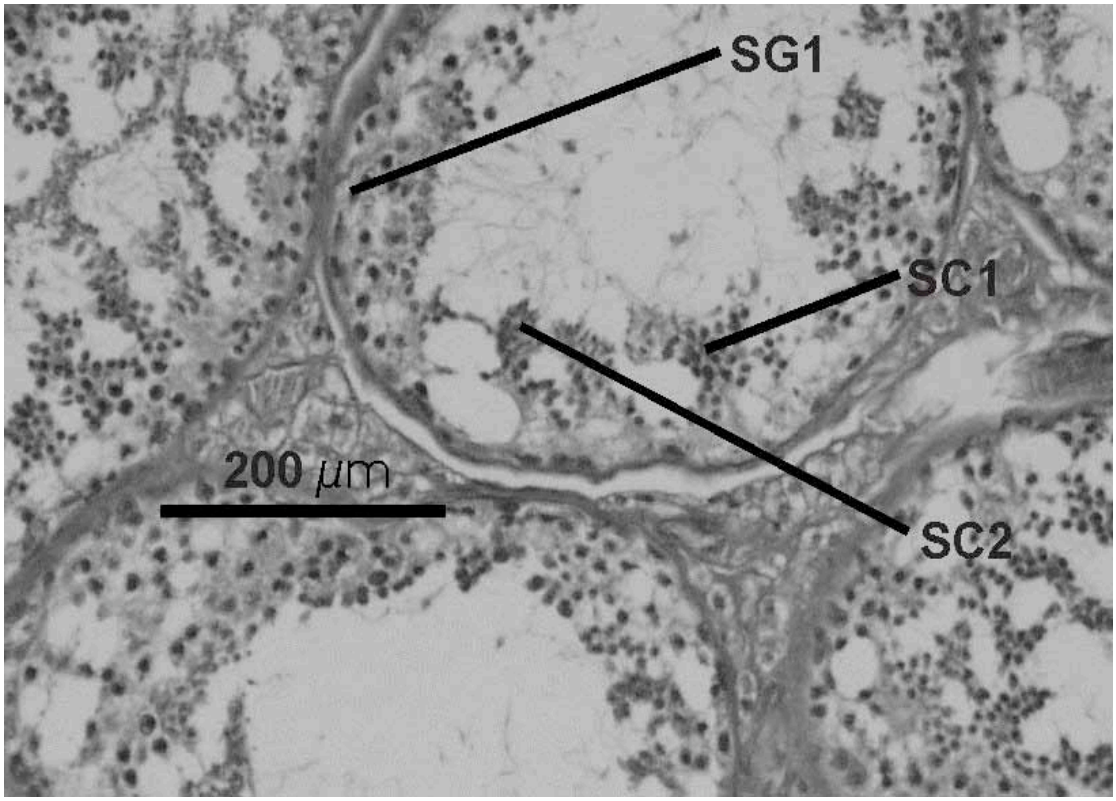


Plate 5.2: Recrudescent *V. mertensi* testis showing primary spermatogonia cells (SG1), primary (SC1) and secondary (SC2) spermatocysts.

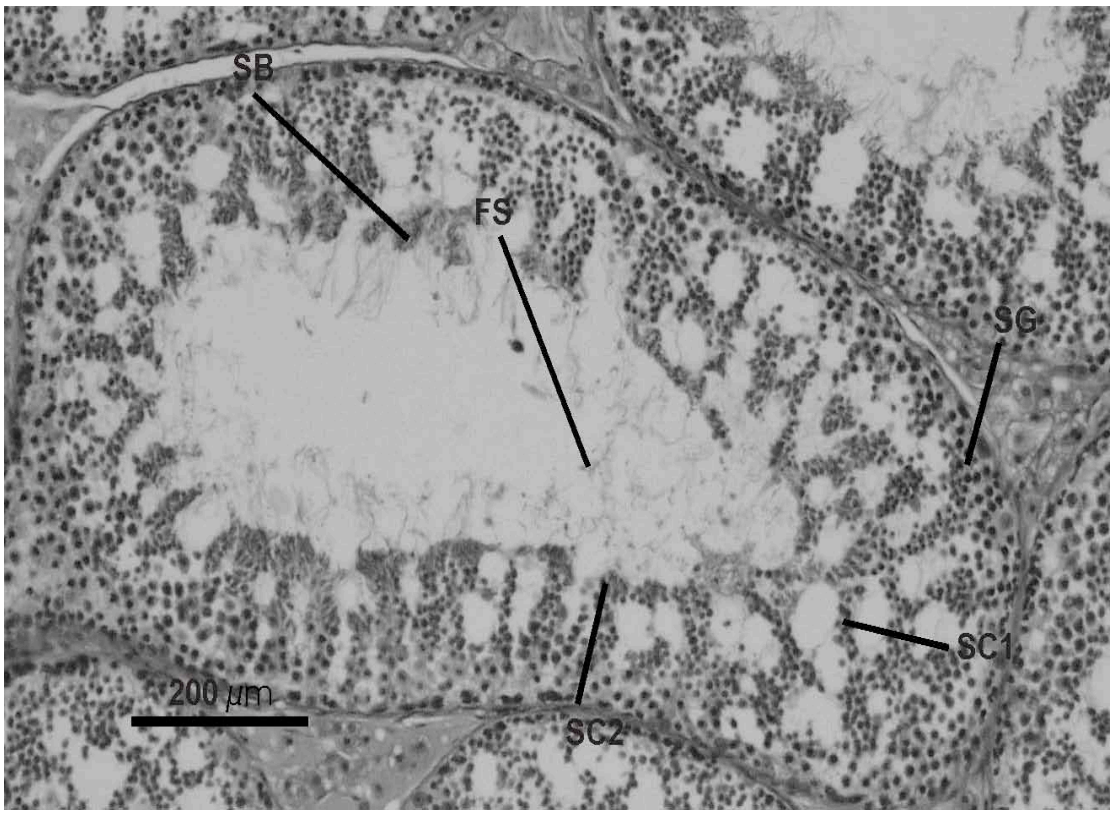


Plate 5.3: Recrudescent *V. mertensi* testis showing primary spermatogonia cells, Primary (SC1) and secondary (SC2) spermatocysts, sperm bundles (SB) and free sperm (FS).

5.4.5 Measurement of hormones

Reproductive hormones in blood plasma samples were measured following the methods of Bradshaw *et al.* (1991) and employed chromatographic separation of An from E_2 following the protocol of Fairclough *et al.* (1977). The 64 plasma samples (10 µl) were first assayed for An levels using the radioimmunoassay outlined in the following sections but without prior chromatographic treatment. This was an essential step as there was more than a thousand-fold difference among the concentrations of An in males. Prior indication of the level of An likely to be encountered enabled a suitable fraction of the An extract to be carried through the assay (following sections).

Extraction and purification of steroids using column chromatography

For the estimation of procedural loss of steroids throughout purification, trace amounts of [1,2,6,7-^{3}H] testosterone and [2,4,6,7-^{3}H] E_2 (Amersham, Buckinghamshire, UK) in assay buffer (0.01 mol phosphate buffered saline) (PBS) were first added and mixed with plasma samples. Steroids were extracted from plasma (200 µl) using two volumes of 2.5 ml di-ethyl ether (BDH Laboratory Supplies, Poole, U.K.) with 1 min vortexing. The supernatants were combined and dried at 37 ^{o}C under compressed air. Dried extracts were redissolved in 0.5 ml column solvent (CS) (n-hexane: chloroform, 8:2; BDH Laboratory Supplies, Poole, U.K.) and applied to glass mini-columns (1 cm in diameter) packed with 5 ml Lipidex™-5000 (Packard Instruments, Meriden, CT, USA) suspended in CS. A further 2 x 0.5 ml washings of extract were added to the column and the load volume (1.5 ml) was discarded. A further 2 ml were eluted and discarded, and the next 5 ml, containing the purified An (see Figure 5.1) were collected in a graduated glass tube. Mean recovery of An throughout all assays was 74.06% ± 0.99 (n=8). After changing the CS (n-hexane:chloroform; 3:7), E_2 was eluted in the fraction 7 – 17 ml CS (see Figure 5.1). Mean recovery for E_2 throughout all assays was 62.42% ± 0.81 (n = 8). Each fraction (5 or 10 ml) was carefully mixed and 1 ml was pipetted into scintillation vials, dried under compressed air and 3.0 ml of scintillant (Ultima-Gold, Packard Instruments, Meriden, CT, USA) added to calculate recovery. With regard to the preliminary levels of total An measured, the remaining (4 ml) An fraction was sub-divided into 0.1, 0.5 and 3.4 ml aliquots. The 9 ml E_2 fraction remained

undivided and all eluate fractions were dried under compressed air at 37 °C and assayed.

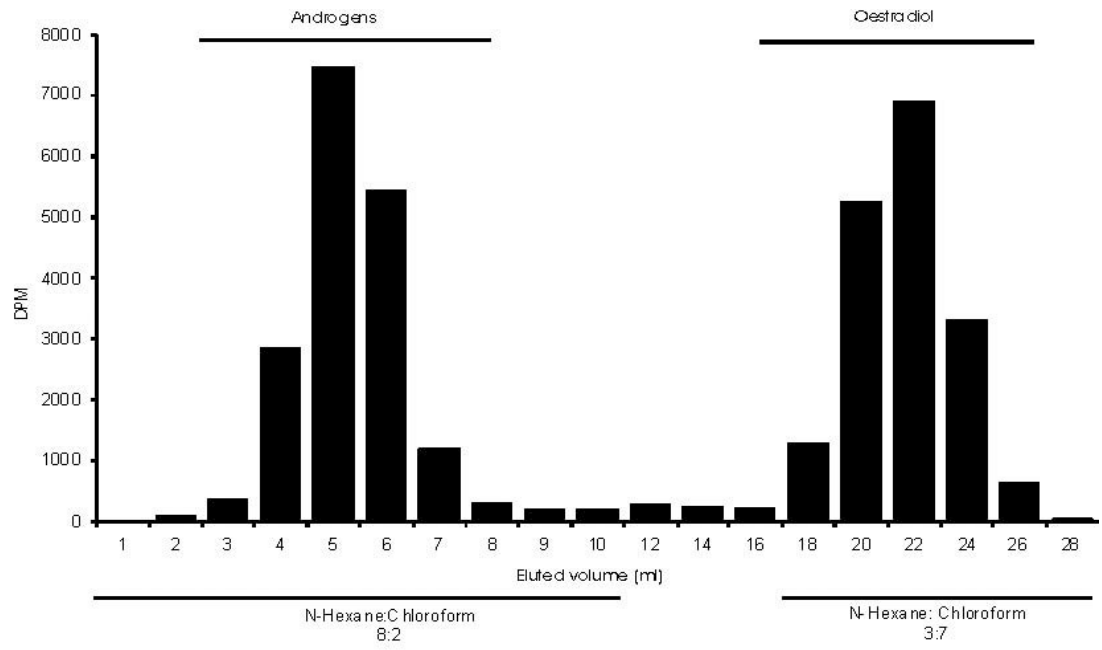


Figure 5.1: Column elution graph for both androgens (An) (testosterone and 5α-dihydrotesterone) and oestradiol-17β (E_2). Column solvents used to elute both steroids are shown. DPM = disintegrations per minute.

Radioimmunoassay

Dried An extracts were redissolved in assay buffer (PBS, containing 0.5% BSA from Sigma Chemicals, St Louis, USA) and incubated overnight at 4 ºC with 133 Bq [1,2,6,7-^{3}H] testosterone and testosterone antiserum (Sirosera^{TM} C-0457; Bioquest Ltd, North Ryde NSW). Cross-reactivity of the antiserum, reported by the manufacturers, was 100% with testosterone, 98% with 5α-dihydrotestosterone, 47% with androsten-3β and androsten-17β-diol, 4.7% with androstenedione, and < 1% with progestagens and oestrogens.

Dried E_2 extracts were also redissolved in assay buffer and incubated overnight at 4 ºC with 133 Bq [2,4,6,7-^{3}H] E_2 and E_2 antiserum (Sirosera^{TM} C-9757; Bioquest Ltd, North Ryde, NSW). Cross-reactivity of the antiserum was 100% with oestradiol-17β, 1% with oestrone, oestradiol-17α and oestriol, and < 0.1% with testosterone, progesterone and corticosteroids. Standard amounts of testosterone and E_2 were incubated in duplicate alongside the samples.

Following incubation, the standards and samples were cooled to 0-2 ºC before addition of 5 mg of Norit A acid-washed charcoal (ICN Pharmaceuticals, USA) with

0.5 mg dextran T_{500} (Pharmacia Chemicals, Uppsala, Sweden) to separate bound from free steroid. After centrifugation, an aliquot of supernatant was measured for radioactivity in a Packard Tri-Carb 2300TR Liquid Scintillation Analyser with quenching corrected by automatic external standardisation and all samples counted to 1% error. Standards were transformed using a 4-parameter logistic curve and, after correcting for procedural loss, An and E_2 levels were expressed in ng ml^{-1} plasma.

Validation

Inter-assay variation was determined by including a sample consisting of standard amounts of testosterone and E_2 added to steroid-free *V. mertensi* plasma with each assay. Inter-assay variation of An was 17.3 % (n = 5) and 25.8 % (n = 5) for E_2. Intra-assay variation was determined by measuring 6 of the above standards in the one assay. Intra-assay variation of An was 26.7 % (n = 5) and 30 % (n = 6) for E_2.

The sensitivity of the assays was estimated to be between 0.05 ng ml^{-1} and 150 ng ml^{-1} for An and >0.06 ng ml^{-1} for E_2, using the method of Frankel *et al.* (1967).

5.5 Results

5.5.1 Sexing *V. mertensi*

The sex of all 62 different adult *V. mertensi* sampled during the field study was determined using a combination of the two techniques. The sex of 46 adult *V. mertensi* (74.2%) was determined to be male and 16 (25.8%) female. This represents an approximate 3:1 male biased sex ratio most likely reflecting capture techniques used in this study.

Of the males, the sex of 24 (52.2%) was confirmed by both the field-based hemipenile eversion technique and hormone ratio; the sex of 17 (35.4%) was determined using only the hormone ratio and the sex of 5 (10.86%) was determined using only field-based hemipenile eversion (Table 5.1).

Of the females the sex of 9 (56.3%) was confirmed by both the field-based hemipenile eversion technique and the hormone ratio; the sex of 5 (31.2%) was determined using only the hormone ratio and the sex of 2 (12.5%) was determined using only field-based hemipenile eversion (Table 5.1).

Table 5.1: Androgen (An) and oestradiol-17β (E_2) levels in plasma collected from 62 different adult (snout-vent length >370 mm) *Varanus mertensi*. An levels < 0.05 ng ml^{-1} denoted UD (undetectable), E_2 levels < 0.06 ng ml^{-1} denoted UD. An levels undetectable >150 ng ml^{-1} denoted >150. Ratio of An: E_2 and sex indicated by ratio shown as males for a ratio > 1, females for a ratio <1 and (-) ratio inconclusive. Field sex determined through eversion of male hemipenes. Final sex of individuals determined by a combination of An: E_2 ratio and field sex. Notes indicate (1) Confirmed; field sex and ratio concur, (2) Field; field sex alone used to determine final sex, (3) Ratio; ratio alone used to determine final sex.

Animal #	An ng.ml $^{-1}$	E_2 (ng.ml $^{-1}$)	An: E_2	Field	Ratio	Final	Notes
2	3.04	0.18	17.19	0	♂	♂	Ratio
3.17	4.37	0.10	41.8	♂	♂	♂	Confirmed
7	46.35	0.22	206.54	♂	♂	♂	Confirmed
8	>150	0.22	High	♂	♂	♂	Confirmed
5	82.93	0.43	192.43	0	♂	♂	Ratio
9	0.45	0.31	1.47	♂	-	♂	Field
13	0.07	0.58	0.119	0	♀	♀	Ratio
12	0.08	1.3	0.06	0	♀	♀	Ratio
1.8	16.11	0.11	145.04	0	♂	♂	Ratio
1.12	0.06	2.12	0.03	♀ (gravid)	♀	♀	Confirmed
1.9	0.12	1.11	0.106	♀	♀	♀	Confirmed
1.14	3.87	UD	High	♂	♂	♂	Confirmed
1.13	0.09	0.37	0.242	♀	♀	♀	Confirmed
2.14	0.098	1.88	0.052	0	♀	♀	Ratio
2.6	0.109	0.44	0.248	0	♀	♀	Ratio
2.13	0.076	1.00	0.075	♀	♀	♀	Confirmed
2.15	26.74	UD	High	♂	♂	♂	Confirmed
2.16	51.34	0.20	256.54	♂	♂	♂	Confirmed
2.17	19.26	0.15	132.9	♂	♂	♂	Confirmed
2.18	0.81	0.22	0.367	♀	♀	♀	Confirmed
3.6	0.42	0.96	0.436	♀	♀	♀	Confirmed
5.7	3.29	UD	High	♂	♂	♂	Confirmed
3.1	1.94	0.16	12.48	♂	♂	♂	Confirmed
3.13	104.11	0.25	412.57	0	♂	♂	Ratio
3.14	0.283	0.10	2.71	0	♂	♂	Ratio
3.15	61.09	0.22	275.60	0	♂	♂	Ratio
6.2	58.71	0.12	498.94	♂	♂	♂	Confirmed
3.16	UD	0.20	-	♀	-	♀	Field
3.18	4.46	UD	High	0	♂	♂	Ratio
3.19	97.36	0.20	478.34	0	♂	♂	Ratio
3.2	135.88	0.13	1073.1	♂	♂	♂	Confirmed
4.6	3.45	0.15	22.67	♂	♂	♂	Confirmed
5.7	UD	UD	-	♀	-	♀	Field
4.9	UD	0.89	Low	♀	♀	♀	Confirmed
4.11	>150	0.14	High	0	♂	♂	Ratio
4.13	>150	0.87	High	♂	♂	♂	Confirmed
4.14	>150	0.49	High	♂	♂	♂	Confirmed
4.15	45.97	0.14	325.17	0	♂	♂	Ratio
14	5.97	UD	High	♂	♂	♂	Confirmed
4.16	30.08	UD	High	♂	♂	♂	Confirmed
4.17	UD	0.29	-	♂	-	♂	Field
4	4.85	UD	High	0	♂	♂	Ratio
5.6	59.54	0.24	251.76	♂	♂	♂	Confirmed
4.19	24.39	UD	High	♂	♂	♂	Confirmed
5.11	UD	UD	-	♂	-	♂	Field
5.13	8.56	UD	High	0	♂	♂	Ratio
5.14	UD	0.51	-	♂	-	♂	Field
5.16	42.32	0.22	196.42	0	♂	♂	Ratio
5.18	UD	0.62	Low	♀	♀	♀	Confirmed
5.19	38.07	UD	High	♂	♂	♂	Confirmed
6.1	UD	0.53	-	♂	-	♂	Field
6.2	20.89	UD	High	♂	♂	♂	Confirmed
6.4	33.01	0.27	121.08	0	♂	♂	Ratio
6.5	20.84	0.18	117.52	♂	♂	♂	Confirmed
6.6	134.5	0.21	641.18	♂	♂	♂	Confirmed
6.8	32.88	0.16	205.02	0	♂	♂	Ratio
6.7	10.52	0.15	69.25	♂	♂	♂	Confirmed
6.9	0.07	1.7	0.043	0	♀	♀	Ratio
6.11	26.34	0.24	109.24	0	♂	♂	Ratio
6.12	54.92	0.24	230.34	0	♂	♂	Ratio
6.10	4.94	0.22	22.6	♂	♂	♂	Confirmed
6.13	UD	1.38	Low	♀ (gravid)	♀	♀	Confirmed

5.5.2 Androgens in chromatographed and unchromatographed plasma

There was a significant positive correlation between total An levels obtained through screening of unpurified plasma and An levels determined through RIA of chromatographically-purified plasma samples ($y = 1.6511x + 4.8139$, $r^2 = 0.843$, $P < 0.001$; Figure 5.2). Unchromatographed values were approximately double those obtained following chromatographic separation and purification of the steroids. This would suggest that impurities, in unchromatographed plasma, yields overestimates of androgen levels, highlighting the importance of using Lipidex™-5000 (Packard Instruments, Meriden, CT, USA) column chromatographic separation in RIA analysis of *V. mertensi* plasma.

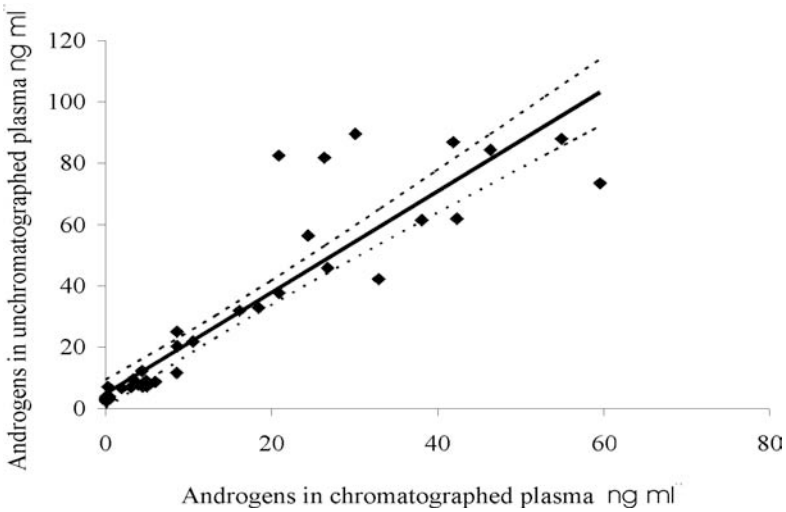


Figure 5.2: Androgens levels in chromatographed *V. mertensi* blood plasma compared with unchromatographed plasma. Regression line (see text for equation) and 95% confidence limits shown.

5.5.3 Field observations

Three mating attempts were observed during the field study. One mating attempt was observed during December and two during February. Two obviously gravid females were also captured during January.

5.5.4 Seasonal variation in hormone levels

The concentration of An in plasma taken from males ranged from below the detectable level of 0.05 ng ml^{-1} (ND) (n = 5) to greater than 150 ng ml^{-1} (n = 4). Using these limit values for those samples outside the measurable range, the mean concentration of An was 40.3 ng ml^{-1} ± 6.9 (n = 48). In comparison, mean concentration of An in females was approximately 400-fold less, with a mean of 0.09

ng ml^{-1} ± 0.02 (n= 16) ranging from ND (n = 5) to 0.41 ng ml^{-1} (n =1). The mean concentration of E_2 in plasma from males was 0.18 ng ml^{-1} ± 0.02 (n = 48), and ranged from below the detectable level of 0.06 ng ml^{-1} ND (n = 14) to 0.87 ng ml^{-1} (n = 1), whereas in the females, E_2 levels were approximately 15-fold higher, with a mean concentration of 0.93 ± 0.16 ng ml^{-1} (n=16) ranging from ND (n = 1) to 2.1 ng ml^{-1} (n = 1).

Androgen levels of males were elevated during July, August and September with a mean of 123.1 ± 26.9 ng ml^{-1} (n = 4) (Figure 5.3). Comparatively, An levels were lower during months when mating was observed between December – February with a mean of 21.6 ± 7.5 ng ml^{-1} (n = 23) (Figure 5.3). Three of the four samples that were above the upper detectable limit of the assay (150 ng ml^{-1}) were recorded during July, August and September. Only one other sample found to have an androgen level above 150 ng ml^{-1} was recorded outside these months, during January, (11 other samples taken during January). Mean E_2 levels in females were elevated between December - February, with two high values also in April and July (Table 5.2).

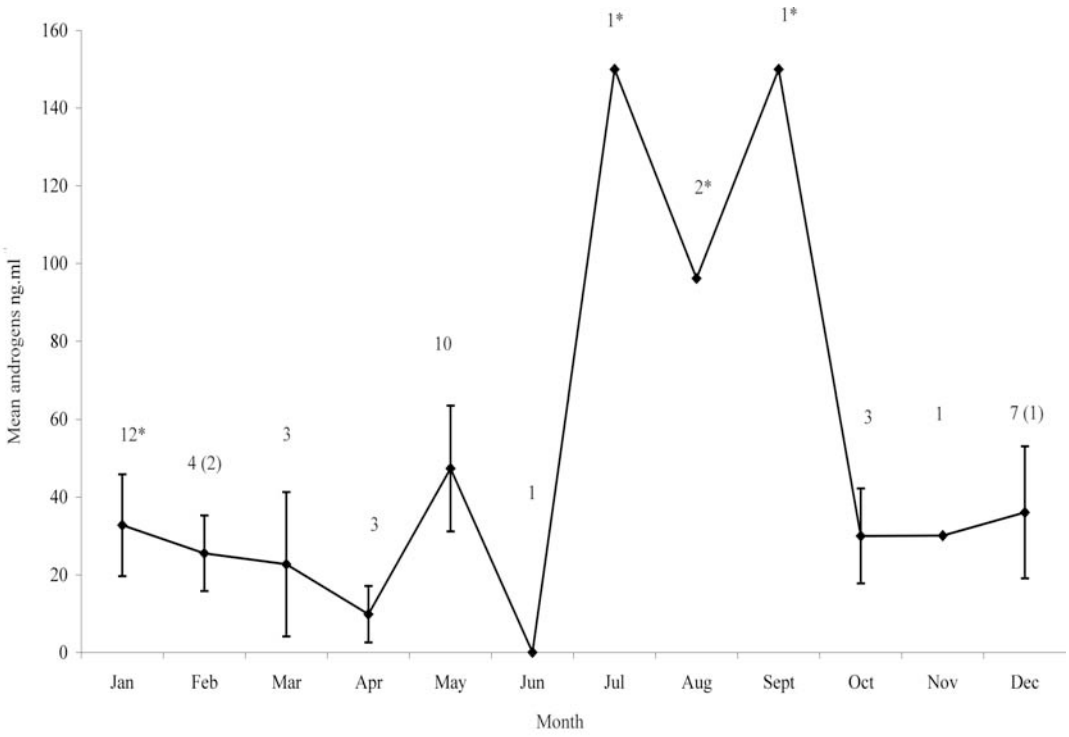


Figure 5.3: Monthly mean androgen levels (± one standard error) for male *V. mertensi*. Androgen levels measured in 48 plasma samples taken from 46 different adult male *V. mertensi* (SVL ≥ 370 mm) sampled over the years 2001, 2002 and 2003 in the East Kimberley. Numbers in parentheses represent number of observed mating attempts, * depicts androgens levels > 150 ng ml^{-1} recorded.

Table 5.2: Mean oestradiol-17β levels (± one standard error) in female *V. mertensi*. Oestradiol-17β levels measured in 16 plasma samples taken from16 different adult female *V. mertensi* (SVL ≥ 370mm) sampled over the years 2001, 2002 and 2003 in the East Kimberley. Capture of gravid egg-carrying adult females in the field indicated by a †. Number of observed mating attempts shown in parentheses. * indicates no plasma samples collected.

Month	n	E_2
January ††	6	1.14 ± 0.25
February (2)	3	1.11 ± 0.42
March	1	0.22
April	1	0.96
May	1	0.21
June	1	0.06
July	1	0.89
August	0	*
September	1	0.62
October	0	*
November	0	*
December (1)	1	1.69

5.5.5 Seasonal variation in gonad size and testes histology

Right and left side testes collected during July were significantly smaller than testes collected during April and October (right; $F_{3,8} = 15.34$, $p = 0.001$; left; $F_{3,8} = 4.99$, $p < 0.05$; Table 5.3). In females, large well-yolked eggs were present in the oviducal tract of specimens collected during December, April and June but the ovaries were small with no enlarging follicles present between July - October (Table 5.4).

Histological examination of 14 testes sections taken from the museum collections showed testes contained free sperm during all months for which specimens were examined except July (Table 5.5). Three of the four testes collected during July were quiescent (see Plate 5.1); with the fourth sample showing early stages of spermatocytogenesis (Plate 5.2) suggesting that recrudescence may begin around this time of year. In support of this, one of four testes collected during August was classified as quiescent whilst the other three all had sperm bundles, two had free sperm, and all three showed evidence of active spermiogenesis (Plate 5.3). Testes collected in September, October, December and April all contained free sperm.

Table 5.3: Volume of *V. mertensi* testes measured in collections held by the Western Australian and Northern Territory museums. Volume corrected per gram of body weight of specimens examined. Number (n) of specimens measured and standard error for each month also given.

Month	n	Volume corrected RHS testes mm^3/ gram	Volume corrected LHS testes mm^3/ gram
April	2	1.77 ± 0.42	1.89 ± 0.62
July	4	0.59 ± 0.13	0.61 ± 0.10
August	4	1.05 ± 0.11	1.21 ± 0.12
September	1	3.01	2.97
October	2	2.71 ± 0.48	1.72 ± 0.49

Table 5.4: Stage of ovarian development in *V. mertensi* specimens held by the Western Australian and Northern Territory museums. Size and volume of oviducal eggs also given.

Month	Stage	Egg size	Volume (mm^3)
April	Undeveloped	Just Visible	
April	Oviducal	Length 61.2mm Width 26 mm	21661.91
June	Oviducal	Length 57.3 mm Width 31.2 mm	29205.35
July	Undeveloped	Round 5.2 mm	87.11
July	Undeveloped	Round 5.7 mm	96.97
July	Undeveloped	Round 9.5 mm	448.92
August	Undeveloped	Round 3 mm	14.14
October	Undeveloped	Round 6.1 mm	118.85
December	Oviducal	Round 37.7 mm	28055.87

Table 5.5: Stage of spermatogenesis in testes sections taken from *V. mertensi* specimens held in collections of the Western Australian and Northern Territory museums. (1) *Quiesescent*, (2) *Recrudescent*, (3) *Sperm bundles*, and (4) *Free sperm*.

Date	Stage
April	2,3,4
April	2,3,4
July	2
July	1
July	1
July	1
August	1
August	2,3,4
August	2,3
August	2,3,4
September	2,4
October	2,3,4
October	2,3,4
December	2,3,4

5.5.6 Emergence of hatchling *V. mertensi*

Given an incubation time in the East Kimberley similar to that reported for *V. mertensi* from captive breeding studies of 260 - 315 days (Eidenmüller 1996), hatchlings should emerge approximately 10 months after egg deposition. If egg deposition occurred during the months of March - June this would suggest that

hatchlings should emerge during the months of January - April of the following year. Field observations in this study support this timing of reproduction. For example, neonate hatchlings (SVL < 200mm) were observed in the field on December 19th in 2001, on February 4th in 2002 and during the period December 15th to January 1st in 2002/3.

5.6 Discussion

5.6.1 Reproductive seasonality of *V. mertensi*

Elevated levels of male sex hormones, sperm production in the testes, and increased testicular volume suggest that males begin sperm production during the dry season months of July and August. Mating attempts in the field, however, were not recorded until the wet season months of December and January. This suggests that males produce sperm in preparation for mating approximately 4-5 months prior to mating commences. Males may store sperm until mating commences during the wet season, which has been reported for other groups of Australian reptiles. Sperm storage has been documented in at least two species of lizards (Amey and Whittier 2000; Smyth and Smith 1968) and several viviparous elapid snakes in Australia, including the Tiger snake, *Notechis scutatus*, that retains sperm in the *vas deferens* all year and mates in both spring and autumn (Shine 1977). It is unlikely that females postnuptially store sperm until the onset of vitellogenesis, after dry season mating, as field observations do not support this. The production of sperm prior to mating by male *V. mertensi* fits the description of an asynchronous or disassociated breeding tactic (Crews 1984a,b).

Elevated levels of female sex hormone, capture of gravid females, and presence of large oviducal eggs suggests their vitellogenesis and mating occurs synchronously during the wet season months of December - February. This concurs with a study by Shine (1986) who suggested that females undergo vitellogenesis and mate during the wet season. Unlike males, the breeding tactic of females fits the description of a synchronous or associated breeding tactic described by Crews (1984a,b). This breeding tactic is similar to that described for numerous other female varanids (James *et al.* 1992).

To date, an asynchronous or disassociated breeding tactic has only been reported for male *V. griseus* in Algeria (Vernet 1977) and *V. griseus koniecznyi*, in Pakistan (Auffenberg *et al.* 1990). Vernet (1977) found that male testes reach a

maximum size in mid May and minimum size in early August. Auffenberg *et al.* (1990) found that males undergo spermatogenesis during the northern winter and early spring between February – April and spermatogenesis occurs after emerging from a period of reduced activity during cooler dry season months between November - February. A similar male breeding tactic used by *V. mertensi* may also be related to seasonal periods of inactivity during the dry season in the wet-dry tropics of Australia (Chapter 6).

The disassociated breeding tactic of male *V. mertensi* is similar to that of many northern hemisphere male reptiles that show periods of reduced activity (Saint Girons *et al.* 1993). For instance, disassociated male breeding tactics have been described for the iguanid *Sceloporous formosus* (Guillette 1985), the Garter snake *Thamnophis sirtalis parietalis* (Crews 1984) and turtles (Callard 1978; Norris 1981). More widely, male disassociated breeding tactics have been reported for other northern hemisphere animals that hibernate over winter such as bats (Crews 1984; Gustafson 1976). It is thought the tactic gives males the capability to mate soon after emerging from periods of inactivity thus retaining the reproductive fitness of males undergoing extended periods of inactivity (Crews 1984).

As males are prepared for mating following the late dry season, the timing of hatchling emergence is partly controlled by the onset of vitellogenesis in females. Pre-emptive production of sperm by males may suggest that the onset of vitellogenesis in females is variable. This may present females with the opportunity to delay vitellogenesis, mating and egg production until after building body condition during periods of high seasonal prey availability. This would allow females to invest a maximum amount of effort into their offspring each year and subsequently give offspring a maximum chance of survival upon emergence. Increased investment in offspring by females has been previously proposed to explain wet season mating and early dry season deposition of eggs in *V. mertensi* and *V. mitchelli* (James *et al.* 1992) and this is further confirmed by this study. Additionally, a long egg incubation time of 9-10 months in *V. mertensi* (Eidenmüller and Wicker 1995; Eidenmüller 1996) may also increase hatchling survival. For example, if eggs were deposited during the early dry season then hatchlings would emerge during the following wet season, providing hatchlings with access to the high wet season prey availability.

5.6.2 Determining the sex of adult *V. mertensi*

A secondary objective of this chapter was to provide a new method for determining the sex of field captured *V. mertensi* using a combining of traditional hemipenile eversion and levels of sex hormones in blood plasma. In this study using a hormone ratio in addition to hemipenile eversion determined the sex of over 50% of males and, more importantly, determined the sex of over 35% of males that were unidentifiable through hemipenile eversion. This shows the importance of using these two techniques to determine the sex of adult *V. mertensi*. This is of particular importance in a remote field situation with limited access to highly specialised equipment. Using a hormone ratio also confirmed the sex of over 50% of females and, more importantly, determined the sex of over 30% that were unidentifiable owing to a lack of hemipenile eversion.

The results of this study strongly support the use of blood plasma sampling from field-captured adult *V. mertensi*. This allows for the subsequent determination of a hormone ratio and the sex of individuals. Traditional hemipenile eversion techniques, however, also proved useful in determining the sex of individuals. Numerous individuals were only identified using this technique owing to undetectable hormone levels (10.9% of males and 12.5% of females). Future studies determining the sex of captured adult *V. mertensi* in remote field localities could adopt a combination of techniques similar to those used in this study. This however, should not detract from the exploration of further alternatives for determining the sex of *V. mertensi* and varanids generally, such as unambiguous sexual dimorphisms but rather should present an alternative technique worth consideration.

-Chapter 6-

Daily and long-term movements of *V. mertensi*

Publications resulting from this chapter

Mayes, P.J (In Press). The use of burrows and burrow characteristics of the semi-aquatic *Varanus mertensi* (Reptilia: Varanidae). *Mertensiella*.

6.1 Summary

6.1.1 Daily movements

Varanus mertensi use overnight refuge burrows located in the banks of waterbodies close to the waters edge. Burrows were also used as escape retreats by disturbed individuals. Burrow entrances were located predominantly on water level, although two burrows were located in rock crevices above water level. Burrows consisted of a gentle upward sloping elongated lumen with a large terminal chamber. Observations suggest that this terminal chamber allows *V. mertensi* to turn around within their burrows. The shape of burrow entrances was flat-bottomed with an arched roofed. Only one burrow had a second entrance, higher up the bank of an irrigation channel above a water level entrance.

After emergence from overnight refuge burrows, *V. mertensi* were observed either basking to elevate core body temperature or immediately entering the water. Individuals also basked for periods during the day to maintain suitable core body temperatures for activity; they basked for 37 % of their total active time. Basking locations included rocks, roads, irrigation infrastructure, floating weed and mud banks, and most were located on the water's edge. Only one individual was observed basking on a rock ledge outside its burrow, away from the water's edge. Basking sites that were chosen facilitated maximum heat gain and prompt resumption of aquatic activity following basking.

Varanus mertensi foraged widely throughout their daily activity areas (14 % of their total active time). Of their total active time, 12 % was spent foraging while swimming and 2 % while walking, showing that *V. mertensi* forages predominantly while swimming. Foraging individuals concentrated their effort along the bank/water

interface of waterbodies. No individual was observed foraging more than 5 m from the water's edge. Individuals were often observed rapidly swimming or walking between different foraging areas at up to 14 m min^{-1}. Speed of movement was highly variable for six *V. mertensi* with a mean of 1.4 ± 0.3 m min^{-1}. The mean daily distance moved by these six *V. mertensi* was 670 ± 270 m and was highly variable with one individual moving up to 2.8 km.

Varanus mertensi concentrated their daily movements within and along the edge of waterbodies; consequently the shape of their daily activity areas reflected the shape of these waterbodies. The mean daily activity area of five *V. mertensi*, observed in irrigation channels, adjoining swamps and farm dams, was 0.65 ± 0.22 ha. In comparison, the mean daily activity area of one *V. mertensi* observed on five different days at the Salerno Gorge main waterhole was only 0.07 ± 0.02 ha. Daily activity areas varied considerably for individuals observed on different days and different individuals.

Individuals were observed to retreat to either the same burrow from which they emerged, or a separate burrow. Individuals usually retreated to a nearby burrow rather than travelling a substantial distance to a burrow just prior to retreat. However, on several occasions individuals rapidly travelled about 500 m to a burrow just prior to retreat. Burrow use by individuals suggested that they were aware of burrow locations within their daily activity areas.

6.1.2 Long-term movements

The shape of long-term activity areas of 37 *V. mertensi*, like the shape of their daily activity areas, reflected the shape of waterbodies. This suggests a highly aquatic lifestyle for *V. mertensi*. However, several individuals moved between waterbodies separated by expanses of terrestrial habitat.

The long-term activity areas of 32 *V. mertensi* found in waterbodies of the ORIS ranged between 0.03 - 31.8 ha. The long-term activity areas of five *V. mertensi* found in natural waterbodies ranged between 0.005 – 0.05 ha. Individuals used core activity areas within their long-term activity areas. Several individuals moved between core activity areas on a seasonal basis. The size of core activity areas ranged between 0.03 – 16.8 ha.

Twenty one percent of radio-tagged *V. mertensi* in both the ORIS and natural waterbodies were found to seasonally burrow for extended periods of inactivity. Dry

season inactivity was not linked to an absence of water given that some water was always present at sites of inactivity. Inactivity was also not linked to low ambient temperature, as numerous individuals remained active throughout the study area during the dry season. This suggests that inactivity may be linked to seasonally low availability of local prey.

Varanus mertensi in both the ORIS and natural waterbodies had overlapping long-term activity areas, suggesting that individuals do not actively defend a territory. Numerous observations of individuals regularly and uneventfully encountering each other during their daily activity also suggests no active defense of territories. Only one combat sequence between two adult *V. mertensi* was observed. The reason for this encounter was unclear, although access to reproductive females was unlikely as the sequence was observed outside the mating season.

Anecdotal evidence suggests that *V. mertensi* have at least two reptile predators; freshwater crocodiles (*Crocodylus johnstoni*) and water pythons (*Liasis fuscus*). However, repeated surveys of an irrigation channel showed that large numbers of both *V. mertensi* and *C. johnstoni* coexist.

6.2 Introduction

The overall aim of this study was to formulate a picture of the ecology and behaviour of *V. mertensi* in the ORIS and surrounding East Kimberley/Victoria River Downs bioregion. To understand the movements of animals it is crucial to first understand other aspects of their ecology and behaviour that may influence their movements. For this reason the movements of *V. mertensi* are considered last in this thesis. This chapter examines the daily and long-term movements of *V. mertensi* taking into consideration findings reported in earlier chapters of this thesis.

6.2.1 Daily movements and behaviour of varanids

Burrow use

Varanids are predominantly diurnal, with few reports of nocturnal activity (Irwin *et al.* 1966; Jones 1998; Valentic 1995). Many different-sized terrestrial and aquatic varanids use refuge burrows both overnight and as an escape retreat when threatened or disturbed (Angelici and Luiselli 1999; Auffenberg 1972; 1983; 1988; Choudbury 1996; Cloudsley-Thompson 1969; De Bitter 1982; Dryden and Wikramanayake 1991; Gaulke *et al.* 1991; Pandau and Whitford 1988; Thompson

1992; Traeholt 1995). However, only a few studies have described the location, size and shape of varanid burrows; these include *V. komodoensis* (Auffenberg 1981), *V. bengalensis* (Auffenberg 1983), *V. griseus* (Tsellarius and Menshikov 1995) and *V. olivaceous* (Auffenberg 1988). Currently only one study has described the location, size and shape of refuge burrows for a semi-aquatic varanid; *V. salvator* (Traeholt 1995). To expand our understanding of the burrows of *V. mertensi* and varanids in general was an objective of this chapter.

Basking sites

Like other reptiles, most varanids behaviourally adjust their core body temperature during activity. Large varanids such as adult *V. komodoensis*, which possess a high thermal inertia, rely to a lesser extent on behavioural modification of core body temperature (Auffenberg 1981a,b). Varanids bask in sunlight to elevate core body temperature to within a narrow preferred temperature range (Bartholomew and Tucker 1964; Christian and Bedford 1995; Christian and Weavers 1996; King 1981; King *et al.* 1983; Stebbins and Barwick 1968; Tsellarius 1997; Wikramanayake and Dryden 1993;). Basking sites used by varanids are generally chosen to facilitate maximum heat gain. The basking sites of semi-aquatic varanids are no exception but are generally located near the water's edge (Gaulke 1999; Jasmin 1988; 1990; Traeholt 1995; 1997a,b). In contrast, the basking sites of terrestrial varanids, such as *V. gouldii*, are generally widely distributed throughout the terrestrial environment (Thompson 1992). To date the basking sites used by the semi-aquatic *V. mertensi* have not been described. To expand our understanding of the basking sites used by *V. mertensi* and varanids in general was another objective of this chapter.

Foraging movements

With several exceptions, such as *V. komodoensis* (Auffenberg 1981; Murphy *et al.* 2002), *V. bengalensis* (Auffenberg 1994) and *V. gleboplama* (Sweet 1999) that have been shown to be predominantly "sit-and-wait" ambush foragers, most varanids are "wide-ranging" active foragers (Dryden and Wikramanayake 1991; James 1996; King *et al.* 1983; Phillips 1995; Thompson 1993; Thompson 1995; Thompson *et al.* 1999; Vernet *et al.* 1988; Yeboah 1993). Semi-aquatic varanids studied to date have also been shown to be "wide-ranging" active foragers of their respective aquatic

environments (Bennett 2000a,b; Cowles 1930; Edroma and Ssali 1983; Gaulke 1989;1991; James *et al.* 1992; Lonnberg 1903; McCoid and Witteman 1993; Modah 1967 Traeholt 1994a,b). In Chapter 4 I described the active opportunistic foraging behaviour of *V. mertensi*. Another objective of this chapter was to expand on this by examining the daily foraging areas of *V. mertensi* further developing our understanding of the foraging behaviour and movements of varanids.

Daily movements

Daily distances moved by foraging varanids vary among species. For example, adults of the medium-sized arboreal *V. tristis* move a daily distance of between 99.7 – 186.5 m (Thompson *et al.* 1999), *V. gouldii* 900 m (Thompson 1992), *V. griseus* between 0.1 – 2.5 km (Vernet *et al.* 1988), *V. komodoensis* 1.8 km (Auffenberg 1981) and *V. salvator* between 252 – 470 m (Gaulke, 1999). Variation in the daily movements of individuals within a species has also been widely reported (Auffenberg 1981; Auffenberg *et al.* 1991; Christian *et al.* 1995; Cloudsley-Thompson 1969; Green and King 1978; King *et al.* 1989; Pandau and Choudbury 1996; Stanner and Mendelssohn 1991; Thompson *et al.* 1999; Traeholt 1997). Another objective of this chapter was to describe the daily movements of *V. mertensi*, furthering our understanding of the daily movements of varanids.

Differences in the location of daily activity areas of semi-aquatic and terrestrial varanids have been reported, with semi-aquatic varanids concentrating their daily movements around water and terrestrial varanids dispersing throughout the terrestrial environment. For example, Gaulke *et al.* (1991) and Traeholt (1997) showed that the daily activity areas of *V. salvator* included flooded palm oil plantations and Angelici and Luiselli (1999) showed that *V. niloticus* remained in the water or on the banks of watercourses. In contrast, Thompson (1992; 1994; 1995) showed that the daily activity areas of the terrestrial *V. gouldii* were dispersed widely throughout a cemetery within a dry urban environment. Another objective of this chapter was to describe the daily activity areas of *V. mertensi* furthering our understanding of the daily activity areas of varanids.

6.2.2 Long-term movement behaviour of varanids

Activity areas and long-term movements

Like the activity areas of many lizards (Christian and Waldschmidt 1984; Turner *et al.* 1969), those of varanids such as *V. gouldii* (Thompson 1994) and *V. komodoensis* (Auffenberg 1981) increase with body size. The size of activity areas has also been shown to vary among varanid species. For example, *V. rosenbergi* have a mean home range of 7.8 ha (Green and King 1978), *V. olivaceus* a mean foraging area of 1.48 ha (Auffenberg 1988), *V. bengalensis* a home range of between 4.4 - 5.3 ha (Auffenberg *et al.* 1991), *V. griseus* a home range of between 31.9 – 98.4 ha (Stanner and Mendelssohn 1987), *V. varius* a mean home range of 65 ha (Weavers 1993), and *V. komodoensis* a mean foraging area of 4200 ha (Auffenberg 1981). Little is known of the activity areas of semi-aquatic varanids. One study of *V. salvator* inhabiting a flooded palm oil plantation reported activity areas of between 1.7 - 22.6 ha (Gaulke *et al.* 1999). Another objective of this chapter was to describe the activity areas of *V. mertensi*, furthering our understanding of semi-aquatic and varanids in general.

Terrestrial varanids move throughout the terrestrial environment (Auffenberg 1972; 1981; 1988; 1994) (Auffenberg *et al.* 1991; Green and King 1978; King *et al.* 1983; Ibrahim 2002; Phillips 1995; Stanner and Mendelssohn 1987; Thompson *et al.* 1999; Thompson 1993; 1995; Weavers 1993). In contrast, semi-aquatic varanids often concentrate their movements around water (Angelici and Luiselli 1999; Auliya and Erdelen 1999; Gaulke *et al.* 1999; Pandav and Choudhury 1996; Traeholt 1997). Likewise, the movements of arboreal varanids are often concentrated within trees, with only occasional on-ground movement from tree-to-tree (Greene 1986; Irwin 1996; Thompson *et al.* 1999). Another objective of this chapter was to describe the long-term movements of *V. mertensi*, furthering our understanding of semi-aquatic and varanids in general.

Numerous varanids use core activity areas within their long-term activity areas. Individuals often move between such areas, using one area for a period before moving onto a new area. For example, *V. gouldii* was found to use foraging areas of 0.03 ha (Thompson 1994), *V. olivaceus*; 0.05 ha (Auffenberg 1988) and *V. rosenbergi*; 1.37 ha (Green and King 1978). The predominantly semi-aquatic *V. salvator* (Gaulke, 1999; Pandav and Choudhury 1996; Traeholt 1994a,b) and *V. niloticus* (Angelici and Luiselli 1999; Cowles 1930) have also been reported using

core activity areas although the size of such areas has not been reported. Another objective of this study was to examine the use of core activity areas by *V. mertensi*, furthering our understanding of the long-term movements of varanids.

Differences in the movements of males and females

Males moving over large distances in search of reproductively receptive females during mating periods has been reported for numerous varanids including *V. tristis* (Thompson *et al.* 1999), *V. komodoensis* (Auffenberg 1981), *V. olivaceous* (Auffenberg 1988), *V. bengalensis* (Auffenberg 1994), *V. glauteri* (Sweet 1999), *V. griseus* (Stanner and Mendelssohn 1987) and *V. gouldii* (Thompson 1994). Another objective of this study was to examine the mating period movements of male and female *V. mertensi*.

Territoriality and combat

Many studies of varanids report a lack of defense of territories or activity areas between neighboring individuals (Auffenberg 1978; 1981b; 1988; 1994; Auffenberg *et al.* 1991). Sweet (1999) however showed territoriality between male *V. glebopalma* suggesting individuals protect prey resources. He also suggested this was important for a "sit-and-wait" forager such as *V. glebopalma* which relies on passing prey resources. Possible territoriality has also been suggested for the arboreal *V. scalaris* although no factor underlying territoriality in this species has been proposed (Sweet, pers. comm.; Pianka *et al.* 2004). Another objective of this study was to examine territoriality amongst *V. mertensi* individuals.

Despite a general absence of territoriality amongst varanids, aggressive combat between individuals has been widely reported for species, including the semi-aquatic *V. salvator* (Daltry 1991), *V. mertensi* (Horn *et al.* 1994; Murphy and Lamoreaux 1978) and numerous terrestrial varanids (Auffenberg 1981; Carpenter *et al.* 1976; Davis *et al.* 1986; Deraniyagala 1958; Mccoid and Hensley 1991, Murphy and Mitchell 1974; Thompson *et al.* 1992; Twigg 1988). In a review of combat behaviour, Horn *et al.* (1994) could not find a common factor leading to combat between individual varanids. Horn *et al.* (1994) also suggested that a "clinch phase" commonly observed between combatants belonging to non-Odatrian taxa had a common phylogenetic origin. Another objective of this chapter was to describe combat behaviour between *V. mertensi*.

Seasonal inactivity

Seasonal inactivity has been reported for several Australian varanids including *V. gouldii* and *V. panoptes* (Christian *et al.* 1995; Christian and Weavers 1996), *V. glebopalma* (Sweet 1999) and *V. rosenbergi* (Green and King 1978). *Varanus rosenbergi* displays different yearly activity patterns in different regions of Australia with inactivity in lower latitudes related to seasonally low ambient temperatures (Green and King 1978). In a study of the tropical *V. glebopalma*, Sweet (1999) suggested that dry season inactivity was linked to a reduction in prey resources rather than seasonally low temperatures. Several authors (Christian and Weavers 1996; Shine 1986) have suggested that *V. mertensi* remain active year round. Another objective of this study is to examine the yearly activity of *V. mertensi*.

Predators

Large varanid species are often considered "top predators", with few if any predators other than humans (Abel 1998; Anon 1983; Auffenberg 1981; 1994; Hensley *et al.* 1994; Inskipp 1984; Shine *et al.* 1996; Traeholt 1998). Medium sized and smaller varanids are often preyed upon by larger predators including other varanids. For example, Browne-Cooper (1998) described a *V. acanthurus* being eaten by a pygmy python (*Antaresia perthensis*) and Christian (1995) reported *V. panoptes* consuming smaller *V. gouldii*. Another objective of this chapter is to identify any predators of *V. mertensi*.

6.3 Aims

The specific aims of this chapter were to:

(1) determine the size, shape and location of overnight refuge burrows;
(2) determine the location and characteristics of basking sites;
(3) determine foraging movements; and
(4) determine the shape and size of daily activity areas;
(5) determine the size of long-term activity areas;
(6) describe long-term movement behaviour and yearly activity;
(7) describe any differences in the movements of males and females particularly during mating season months;

(8) determine if *V. mertensi* display territorialism;

(9) describe combat between individuals; and

(10) identify predators and determine if *V. mertensi* coexist with one possible predator, *C. johnstoni*.

6.4 Materials and methods

6.4.1 Measuring activity areas

In this study 'activity area' is defined as the area used by an animal while going about its day-to-day activities. Numerous techniques are available for measuring the size of activity areas (see following paragraphs). I will refer to the size of activity areas used over the lifetime of an animal as its home range.

Numerous techniques are available for collecting data on the movements of animals over time. Common techniques used for reptiles include cotton spooling where the short-term movements of individuals are tracked following a line of cotton left by active individuals (Bull and Freake 1999; Thompson 1995), and radio-telemetry where radio-transmitters are attached or implanted into individuals and the radio-transmitter radio tracked to determine the position of the individual (Francaz and Vernet 1978; Gaulke *et al.* 1991; Hirth and Latif 1979; Ibrahim 2000; Sokholov *et al.* 1975; Stebbins and Barwick 1968; Sweet 1998; Traeholt 1995). Advances in radio-telemetry technologies have seen this technique used extensively in the study of the long-term movements of varanids (Carter 1999; Green and King 1978; Thompson 1994; 1995).

Numerous techniques are also available for estimating the size of activity areas used by reptiles from movement data (Harris, 1990; Macdonald *et al.* 1980; Rose 1982; Samuel and Garton 1985; Southwood 1978). These include probabilistic techniques, that give an indication of the probability of finding an individual within a given area based on its distribution of positional fixes (Jennrich and Turner 1969). Alternatively, non-probabilistic techniques directly estimate the size of an area used by an individual based on its distribution of positional fixes (Anderson 1982). Both these techniques do not discount areas not used by an individual encompassed by its distribution of positional fixes. This presents a problem when considering data from an aquatic varanid such as *V. mertensi* that concentrates its movements around water and hence has activity areas which resemble the shape of waterbodies.

A different analysis technique was adopted in this study to account for the movements of *V. mertensi* concentrated around water, avoiding the inclusion of areas not used away from water. For example, if an individual was located at two points on a 'U' shaped bend of a linear watercourse then this was considered when measuring activity area so as not to include areas outside the watercourse.

In this study, activity distances along predominantly linear watercourse were measured to avoid including areas away from water not used by *V. mertensi*. Activity area was estimated by multiplying the linear activity distance along the watercourse by the width of the watercourse. This approach has been used previously to analyze the movements of aquatic animals such as platypus (Gardner and Serena 1995; Gust and Handasyde 1995; Serena 1994; Serena *et al.* 2001), crocodiles (Kay 2004; Tucker *et al.* 1997) and river otters (Melquist and Honocker 1983; Somers and Nel 2004)) which also concentrate their movements along linear watercourses.

Irrespective of the technique used to measure activity areas, problems are often still encountered when attempting to report on home range size (Jennrich and Turner 1969; Rose 1982). It is generally recognised that to report home range size long-term movement data spanning the lifetime of an animal should be considered (Jennrich and Turner 1969; Rose 1982). Accordingly, many short-term studies often only report activity area rather than the home range of animals. Presented in this chapter are the long-term movements and activity areas of 37 *V. mertensi* examined over 2 years. The size of *V. mertensi's* home range was not addressed here given the relatively short duration of the study relative to the lifespan of *V. mertensi*.

6.4.2 Measuring the activity areas of *V. mertensi*

In this chapter both the daily and long-term activity areas of *V. mertensi* were first measured as "activity distances". To measure activity distance, all positional data for each individual were plotted onto geo-referenced topographic maps of all study sites using Arcview v. 3.2a. A guide to topographical features displayed on maps can be seen in Key 6.1. Distances were measured directly with Arcview's measuring tool on a visual representation of positional data. If waterbodies used by individuals were not shown on maps, then their position was indicated by a hand drawing. A similar method of visually analysing movements was used to avoid including areas of water not used by terrestrial *V. bengalensis* on the coast of Pakistan (Auffenberg *et al.* 1991).

Activity distances along linear watercourses were measured along the length of watercourses following their path (Figure 6.1). Activity distance for circular waterbodies, such as farm dams and waterholes was measured across the longest diameter of the waterbody used (Figure 6.2). For linear watercourses, activity area was calculated by multiplying activity distance by the width of the watercourse (Figure 6.1). The width of all linear watercourses can be seen in Table 6.1. For circular waterbodies, activity area was calculated as the area of a circle (ΠR^2) where R = radius (longest diameter/2) (Figure 6.2). Total activity areas of individuals using multiple waterbodies were calculated by summing all areas used. Although it is recognised that these estimates of activity area size are only approximate, they are more appropriate for considering the activity areas of the *V. mertensi* examined in this study than alternative techniques.

To examine the use of core activity areas over time by individual *V. mertensi* activity distance accumulated after each subsequent positional fix was measured and plotted (Figure 6.3). Asymptotes in accumulated activity distance suggested the use of a core activity area. This combined with a visual inspection of positional fixes was used to describe core activity areas for each radio-tagged individual.

Table 6.1: The location, name and width of linear watercourses used to calculate activity areas from measured activity distance. Names of watercourses; Ivanhoe Plains Main Irrigation Channel (M1), Ivanhoe Plains Supply Channel 1 (S1), Ivanhoe Plains Supply Channel 2 (S2), Ivanhoe Plains Drainage Channel 1 (D1), Ivanhoe Plains Drainage Channel 2 (D2), Packsaddle Plains Main Irrigation Channel (PSMIC), Four Mile Creek (FMC), Salerno Gorge (SG), Thompson's Spring (TS).

Location	Watercourse name	Width (m)
Ivanhoe Plains Irrigation Area	IPM1	20
	S1	10
	S2	10
	D1	5
	D2	5
	Tangent drainage channels	5
	M1 + S2 combined	50
	M1 + S2 + adjoining swamp combined	100
	M1 + adjoining swamp combined	50
Packsaddle Plains Irrigation Area	PSMIC	10
	Bank of farm dam 1	5
	Bank of farm dam 2	5
Four Mile Creek	FMC	5
Salerno Gorge	SG	30
Thompson's Spring Gorge	TS	5

Key 6.1: Key to topographical features depicted on map images

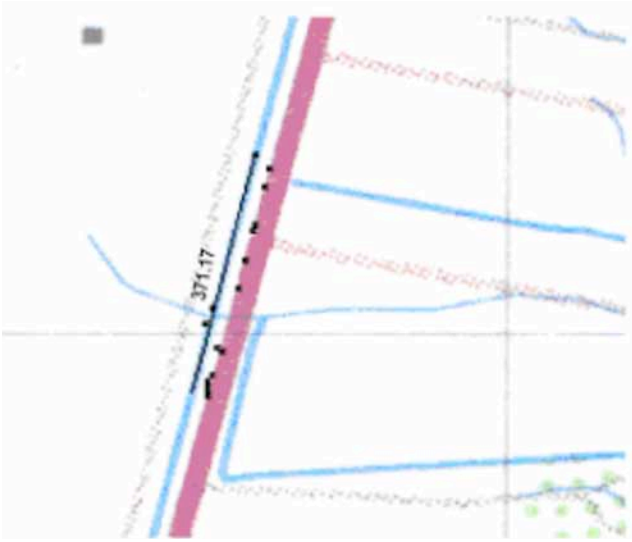


Figure 6.1: The daily movements of animal # 17 on the 21/5/02 in the PSMIC. Daily activity distance along channel 371 m giving daily activity area of 0.37 ha (10 m width of PSMIC).

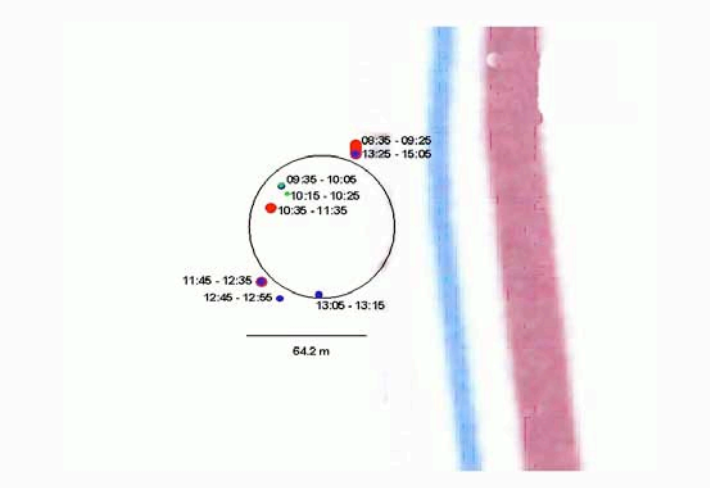
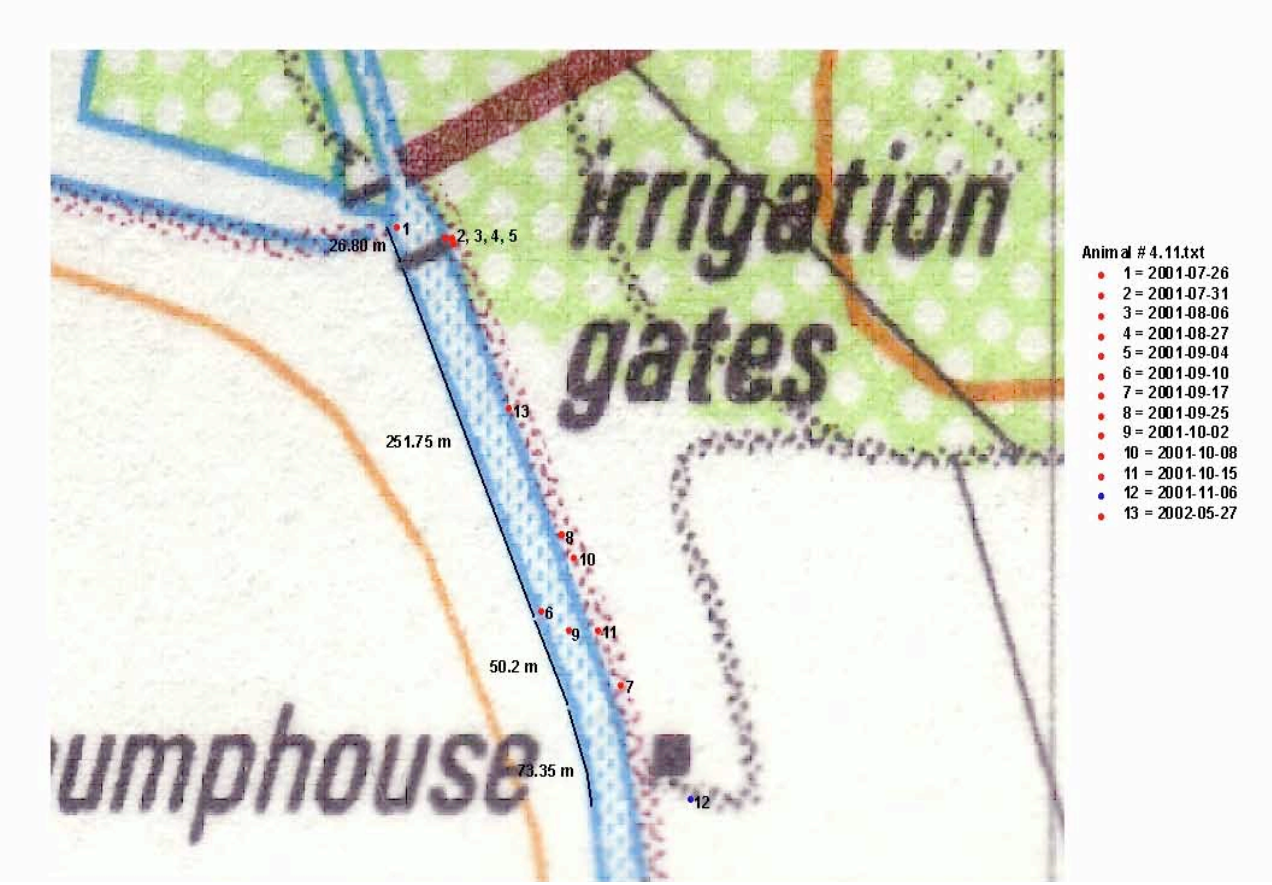


Figure 6.2: The daily movements of animal # 17 on the 28/4/01 in farm dam (circle indicates position of farm dam) adjacent the PSMIC. Diameter of farm dam used 64 m. Daily activity area calculated as 0.03 ha (radius of the farm dam of 32 m).



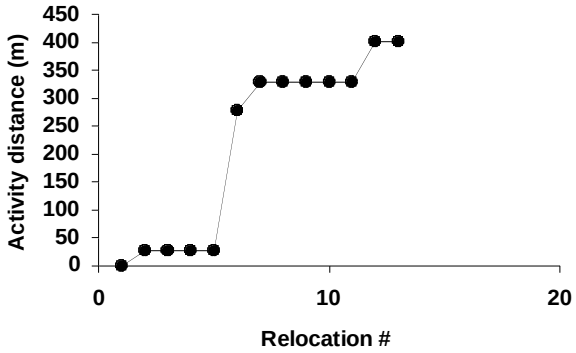


Figure 6.3: Left: Activity distance of animal #4.11 along M1 channel accumulated for each of 13 positional fixes recorded over 10 months. Date each position fix recorded shown in legend. 1 = initial capture and release, after 2 fixes accumulated activity distance = 26.80 m, 6 fixes = 278.55 m, 7 fixes = 328.75 m and 12 fixes 402 m. Right: Activity distance accumulated for each subsequent positional fix after release.

6.4.3 Core activity areas of *V. mertensi*

Core activity area(s) of an individual were defined as the area(s) that it uses most often over time. To identify the core activity areas of *V. mertensi* that concentrates its movements in and around water again is problematic when using traditional techniques. Techniques such as the central 50% of positional fixes assume an individual moves throughout the area encompassed by its positional fixes, which is often not the case for *V. mertensi*. To avoid these problems this study adopted a visually descriptive approach to identify core activity areas used by *V. mertensi*. Core activity areas were identified through visually inspecting maps of the movements of each radio-tagged individual and accordingly activity distance accumulation plots. Core activity areas were first measured along linear watercourses or across the diameter of circular waterbodies and subsequently areas calculated, much like activity areas (see above sections). In doing this it is recognised that for individuals for whom limited long-term movement data were obtained that the number and size of core activity areas may be underestimated. Despite this, it was anticipated that this descriptive analysis would identify if *V. mertensi* use core activity areas and give an indication of the minimum number and size of such areas.

6.4.4 Daily movements

The daily movements, activity areas and behaviour of *V. mertensi* were examined for 25 days during which active radio-tagged individuals were observed for their entire (19 days) or a substantial part of their active day (6 days). Details of methodology and an outline of data collected during each of these observation days are in Chapter 2. Details on dates of observations, location of observations and individuals observed are in Table 6.2 (page 125). No data from partial days of observations were used in the analysis of daily activity areas. However, these data were used to provide a better understanding of the daily behaviour of *V. mertensi*.

Refuge burrow locations and characteristics

Varanus mertensi were observed utilising numerous overnight refuge burrows. The location, size and shape of these burrows were measured. Additional overnight refuge burrows not seen being used by *V. mertensi* were identified using various techniques. Burrow systems from which radio signals emitted and burrows that were determined to be used by nearby *V. mertensi* after assessment for overnight

activity were all measured. Use of a burrow was determined by placing a thin twig across the entrance to burrows near an active *V. mertensi*. Upon revisiting the burrow an individual would move the twig to gain access to the burrow indicating its use to a returning observer.

Ideally, excavation of burrows would allow direct measurement of the length and shape of burrows. This was impractical as most burrow entrances were located on water level, so excavation would drain water from irrigation channels (an undesirable outcome). Consequently, burrow depth and shape were measured indirectly by probing the burrow with a length of 15 mm diameter flexible hose. Burrow shape was determined by gauging the pathway of the flexible hose when inserted along the length of the burrow. Length was taken as the length of flexible hose that could be inserted into the burrow before reaching its terminus. The width and height of burrow entrances was measured directly. Entrance width was measured as the distance between the side walls of the entrance at its lowest point and height the greatest distance between the "floor" and "roof" of entrances. The shape of the burrow entrance was also described.

Daily behaviour

The behaviour of *V. mertensi* was categorised and recorded at 10 minute intervals throughout observation days. Details outlining methodology and behavioural categories are in Chapter 2. The proportion of total daily active time behaving in each category was calculated by totalling the behaviour time in each category and dividing by the total active time for which an individual was observed during its active day.

Basking and foraging locations

Basking behaviour was one category of daily behaviour (see Chapter 2). The position of all basking sites was recorded and shown on maps of daily movements. The locations of preferred basking sites were described based on these data. Field notes on the physical characteristics of these basking sites were used in describing basking site characteristics.

Areas where individuals were observed foraging were also shown on maps of daily movements. Foraging areas were described based on these data and supported by detailed foraging sequences described in Chapter 4.

Speed of movement

Daily speed of movement of observed *V. mertensi* was calculated for all observation days. Daily distance moved by an individual was measured using Arcview v 3.2a along a direct line between consecutive positional fixes. Daily speed of movement was calculated by dividing the total distance moved by walking and swimming during a day by the time taken to move that distance. Periods where individuals remained stationary were included in these calculations. Maximum speed of movement during a day was calculated in a similar fashion for periods where individuals rapidly moved between different areas.

6.4.5 Long-term movements

Long-term activity areas, movements and behaviour of *V. mertensi* were examined through regularly recording the position of 37 individuals during the two years of the field study. Intensive search efforts were undertaken to regularly radio-track all radio-tagged *V. mertensi*. Despite these efforts many *V. mertensi* were lost during the field study. Details of methodology and an outline of data collected from located radio-tagged *V. mertensi* are in Chapter 2. The number of positional fixes and the duration over which they were recorded for each individual are in Table 6.2 (page 125). The date of each positional fix can be seen on figures showing the long-term movements of each individual. Only the position of radio-transmitters determined subsequently to be implanted in a living adult *V. mertensi* were considered in the analysis. Often located radio-tagged *V. mertensi* were not sighted. Such animals were confirmed as alive through a subsequent sighting of an active individual.

Movements of males and females during the mating season

The movements of male and female *V. mertensi* were examined for differences during mating season months. Only individuals with their sex confirmed through both traditional hemipenile eversion and blood hormone levels were considered in this analysis (Chapter 5). Positional fixes of these individuals, recorded during mating season months, were highlighted in pink on maps of long-term movements. Movements during these months were visually compared to movements throughout the remainder of the year and differences described.

Inactive burrowing periods

During the 1st year of the field study numerous radio-transmitters that were assumed to represent healthy adult *V. mertensi* did not move from underground locations for extended periods. To determine if such radio-transmitters represented healthy *V. mertensi* one transmitter was excavated at Thompson's Spring. Individual #2.18 was excavated from an underground burrow healthy (Photograph 6.1a and b). Following the excavation of animal #2.18 no more burrowed inactive *V. mertensi* were disturbed, to avoid interruption of their natural long-term behaviour. At the completion of the study the long-term movements of all individuals were examined for periods of inactivity of greater than 1 week. Positional fixes during such periods were highlighted in yellow on maps of long-term movements.

Plate 6.1a: Location of inactive burrowed adult *V. mertensi* animal # 2.18 excavated on the 2/8/01 from location (52)0494356, 8228013 near Thompson's Spring main waterhole.

Plate 6.1b: Photograph of animal # 2.18 just after excavation from the location seen in Photograph 6.1a.

6.4.6 Interactions with conspecifics and other species

During the field study, antagonistic interactions between *V. mertensi* were described, recorded and photographed. The date, time and any circumstances surrounding such encounters were recorded.

Interactions between *V. mertensi* and other reptiles were also described, recorded and photographed. This included recording details of injuries found on *V. mertensi*. Photographs and anecdotal evidence reporting predation on *V. mertensi* were also collated from the public.

It was anticipated that interactions with other sympatric species such as *C. johnstoni* may influence the long-term movements and behaviour of *V. mertensi*. To examine a possible spatial interaction between *V. mertensi* and *C. johnstoni*, repeated surveys to map the distribution of each species along a section of the main irrigation channel (IPM1) of the Ivanhoe Plains Irrigation Area were completed during 2001, 2002 and 2003. All 2001 surveys for both species were conducted during daylight hours, usually in the morning so as to observe *V. mertensi* while they were basking. It was envisaged that this would maximise the number of individuals sighted, as basking animals are more visible owing to their choice of prominent basking sites. All 2002 and 2003 surveys for *V. mertensi* were also conducted during daylight hours. 2002 surveys for *C. johnstoni* were conducted at night on the day when *V. mertensi* were surveyed after a trial night survey early in 2002, indicated more *C. johnstoni* were sighted at night based on eyeshine than were sighted basking during the day.

All surveys were conducted from a slow moving vehicle (5 km hr^{-1}) driven along 12 km's of access road adjacent to the IPM1 channel. Both species were counted when sighted from the moving vehicle. Animals were counted if they were seen on either the channel bank, in the water or on channel access roads on either side of IPM1. The location of sighted animals along the section of IPM1 Channel was recorded using the vehicle's odometer. Odometer readings were referenced back to a common zero point at the beginning of the IPM1 Channel for all surveys. The same vehicle, with consistent odometer readings was used for all surveys.

6.4.7 Recordings of water flow at study sites

It was envisaged that the long-term movement behaviour of *V. mertensi* may also be affected by the availability of water within various waterbodies of the ORIS.

Authorities regularly change water flow within irrigation watercourses of the ORIS. To examine this, water availability in both irrigation areas was recorded throughout the field study. Water levels were recorded on a weekly basis at numerous points in the Ivanhoe Plains and Packsaddle Plains irrigation areas. Both *in situ* measuring boards installed by water authorities and fixed reference points within irrigation channels were used for measuring water levels.

6.5 Results

The long-term movements of 37 adult radio-tagged *V. mertensi* including individuals found in irrigation waterbodies of the Packsaddle and Ivanhoe Plains Irrigation Areas and the natural watercourses of Four Mile Creek Gorge, Salerno Gorge, Thompson's Spring Gorge and Alligator Creek Gorge are presented in the following sections. The daily movements and behaviour of seven of these 37 *V. mertensi* observed on a total of 25 days are also presented. Nineteen of these days show daily movements of individuals in waterbodies of the ORIS, and six days show daily movements of animal #5.14 in the main pool of Salerno Gorge. Data on the long-term and daily movements of all individuals are summarised in Table 6.2 (page 125).

To build a picture of the movements of *V. mertensi*, each radio-tagged individual is considered separately in the following sections. Presented first are the long-term movements of each individual. Areas used during all daily observations of each individual are also indicated on maps showing long-term movements. This is followed by a map showing the daily movements of each individual on the days for which it was continually observed. It is envisaged this will show common trends in the movements of all *V. mertensi* examined. The structure of data presented for each radio-tagged individual has been standardised and includes:

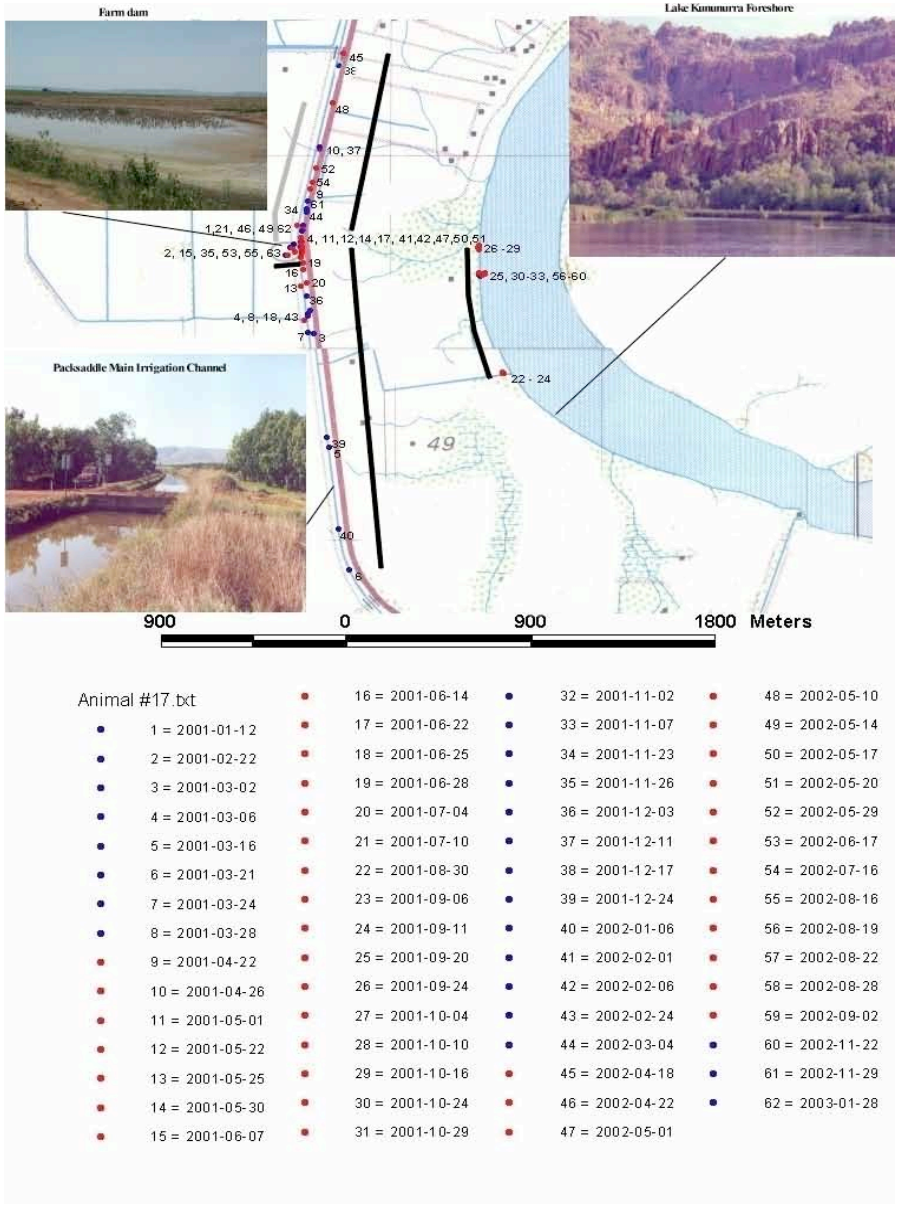
(1) *Long-term movements*: Snout-vent length (SVL), sex (UC = unconfirmed), map of site showing key waterbodies, plates showing key areas, date and position of capture and release (1), dates and position of subsequent radio-fixes, positional fixes during mating season months (pink), wet season months (blue), dry season months (red), core activity areas (black bars), areas utilised during daily activity observations (grey), description of long-term movements, activity distance accumulation plot and a table summarising activity areas and core activity areas.

(2) *Daily movements*: Map of site, position and behaviour of individual at 10 minute intervals (see Key 6.2 for colour coding of position fixes for different behaviours), daily activity distances and area, description of daily movements and table summarising daily behaviour.

Key 6.2: Key to behaviour of observed individuals.

Table 6.2: Site at which *V. mertensi* found, individuals snout-vent length (SVL), sex, number of radio-fixes or date of observation day; duration over which radio-fixes recorded or time for which an individual observed. Data represented in figures shown as long-term (LT) movement data and daily (D) observation data.

Animal #	Site	SVL	Sex	Data	Radio-fixes/ date	Dates/ times	Figure
17	PS channel/ Lake Knx	370	unconfirmed	LT	82	12/1/01-28/1/03	6.4
"	Dam/ PS channel	"	"	D	28/4/01	8:35-15:05	6.5
"	PS channel	"	"	"	29/5/01	9:15-14:25	6.6
"	Dam/ PS channel	"	"	"	5/2/02	8:25-17:05	6.7
"	"	"	"	"	12/3/02	7:10-12:50	6.8
"	"	"	"	"	19/4/02	6:40-17:40	6.9
"	"	"	"	"	23/4/02	6:30-16:00	6.10
"	"	"	"	"	21/5/02	7:10-16:00	6.11
"	"	"	"	"	18/6/02	7:00-17:20	6.12
"	Dam	"	"	"	23/7/02	8:00-17:00	6.13
"	Dam/PS channel	"	"	"	23/11/02	6:30-11:10	6.14
1.7	PS channel/ Lake Knx	430	"	LT	90	13/1/01-30/1/03	6.15
"	Dam	"	"	D	29/1/03	10:00-15:40	6.16
"	Channel	"	"	"	31/1/03	7:30-15:30	6.17
"	Dam	"	"	"	2/2/03	6:50-16:20	6.18
15	M1	430	"	LT	28	12/1/01-12/2/02	6.19
5	"	470	"	LT	27	10/1/01-10/9/01	6.20
1	M1/ S2	535	"	LT	47	12/1/01-12/2/02	6.21
12	"	390	"	LT	42	11/1/01-22/3/02	6.22
6	M1/Lake Knx	390	"	LT	42	9/1/01-27/5/02	6.23
1.8	"	420	"	LT	40	14/1/01-15/10/02	6.24
1.16	PS channel/ Lake Knx	450	"	LT	79	17/1/01-28/1/03	6.25
11	M1	400	unconfirmed	LT	59	11/1/01-15/5/02	6.26
1.13	"	420	♀	LT	49	16/1/01-4/2/02	6.27
7	"	470	♂	LT	49	10/1/01-17/4/02	6.28
8	"	500	♂	LT	42	10/1/01-10/7/02	6.29
"	"	"	"	D	19/1/01	9:30-17:00	6.30
"	"	"	"	"	10/12/01	9:05-10:25	6.31
20	"	420	unconfirmed	LT	35	13/1/01-17/6/02	6.32
1.14	"	390	♂	"	35	16/1/01-17/9/01	6.33
4.9	"	460	♀	"	28	24/7/01-24/2/02	6.34
2.6	"	510	unconfirmed	"	23	16/2/01-17/7/01	6.35
2.8	PS channel	390	unconfirmed	"	22	20/1/01-20/9/01	6.36
2.13	M1	500	♀	"	21	15/2/01-27/11/01	6.37
16	M1/S2	460	unconfirmed	"	18	12/1/01-5/6/01	6.38
4.16	M1	370	♂	"	17	14/11/01-4/7/02	6.39
4	M1/S2	450	unconfirmed	"	16	9/1/01-29/1/02	6.40
5.16	M1	400	unconfirmed	"	14	19/8/01-25/1/03	6.41
"	"	"	"	D	16/1/03	7:00-17:00	6.42
"	"	"	"	"	20/1/03	7:00-16:50	6.43
4.11	"	550	unconfirmed	LT	13	26/7/01-27/5/02	6.44
4.14	"	450	♂	"	13	10/9/01-11/12/01	6.45
3.14	Four Mile Creek	400	unconfirmed	"	13	25/7/01-21/11/01	6.46
1.9	M1	385	♀	"	12	14/1/01-30/3/03	6.47
4.6	Alligator Creek Gorge	440	unconfirmed	"	12	16/6/01-31/10/01	6.48
3.18	"	430	unconfirmed	"	11	10/6/01-20/10/01	6.49
5.18	M1/S2	460	♂	"	11	3/10/02-23/1/03	6.50
2	M1	420	unconfirmed	"	11	9/1/01-11/12/01	6.51
18	PS channel/Lake Knx	450	unconfirmed	"	9	12/1/01-29/10/01	6.52
5.14	Salerno Gorge	380	♂	"	7	6/6/02-30/11/02	6.53
"	"	"	"	D	13/6/02	8:30-16:30	6.54
"	"	"	"	"	14/6/02	7:50-17:30	6.55
"	"	"	"	"	2/7/02	8:10-17:00	6.56
"	"	"	"	"	31/7/02	8:10-16:40	6.57
"	"	"	"	"	30/11/02	7:40-9:30	6.58
"	"	"	"	"	1/8/02	7:20-16:40	6.59
3.20	PS channel	400	unconfirmed	LT	24/9/01-29/1/01		6.60
"	"	"	"	D	21/9/01	9:00-9:50	6.61
2.10	M1/S2	380	unconfirmed	LT	6	23/1/01-8/3/01	6.62
1.15	PS channel	390	unconfirmed	"	7	17/1/01-22/4/01	6.63
"	"	"	"	D	18/4/01	9:25-17:45	6.64
2.18	Thompson's Spring	450	♀	LT	7	15/3/01-3/10/01	6.65



Animal #17

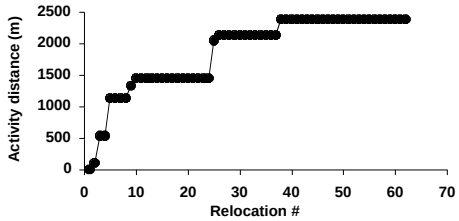


Figure 6.4: Left: Long-term movements of animal #17 (SVL = 370 mm, Sex = UC) in the Packsaddle Main Irrigation Channel (PSMIC) and along Lake Kununurra Foreshore (LKF), circle indicates the position of a perennial farm dam 1 adjacent the PSMIC. Areas used during all daily observations also indicated (grey). Above: Activity distance accumulated after each subsequent positional fix following release.

Table 6.4: Length, width and area of total activity areas and core activity areas (CAA).

Site	Total Length (m)	Width (m)	Area (m^2)	CAA length (m)	Width (m)	Area (m^2)
Channel	1686	10	16860	1686	10	16860
Dam	76		4536	76		4536
Foreshore	688	10	6880	688	10	6880

Long-term movements: Animal #17 used three core activity areas a length of PS channel, a farm dam adjacent the PSMIC and a length of LKF. It remained within its PSMIC and farm dam core activity areas for a period of approximately 7 months from the 12/1/01 - 30/8/01. It was only found outside these areas between the 16/3/01 – 21/3/01. It moved to its LKF core activity area on the 30/8/01 for a period of two months. It returned to its PSMIC core activity areas on the 7/11/01 for a further 9 months and was only found outside this area between the 17/12/01 – 6/1/02 and the 18/4/02 and 10/5/02. In 2002 it again returned to its LKF core activity area on the 19/8/02. It remained in this area for approximately 3 months before moving back to its PSMIC core activity areas on the 29/11/01 where it was found until the completion of the study.

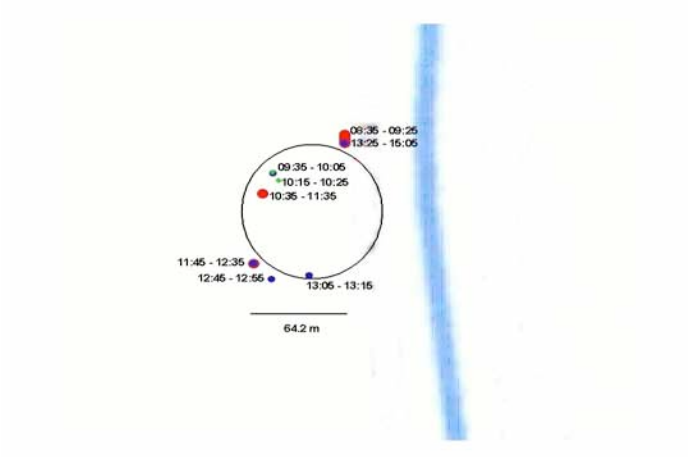


Figure 6.5: Daily movements of animal #17 in farm dam 1 adjacent the PSMIC on the 28/4/01.

Table 6.5: Areas where different behaviours were undertaken and their duration.

Behaviour	Time (mins)	Location
Basking	110	Banks of dam
Swimming	130	Dam
Walking	80	Banks of dam

Daily movements: Included a large section of farm dam 1 with a diameter of 64 m and area 3237 m². Individual remained within farm dam 1 throughout the day. Distance moved 219 m equating to a speed of 0.56 m min^{-1}. No burrow locations observed being used.

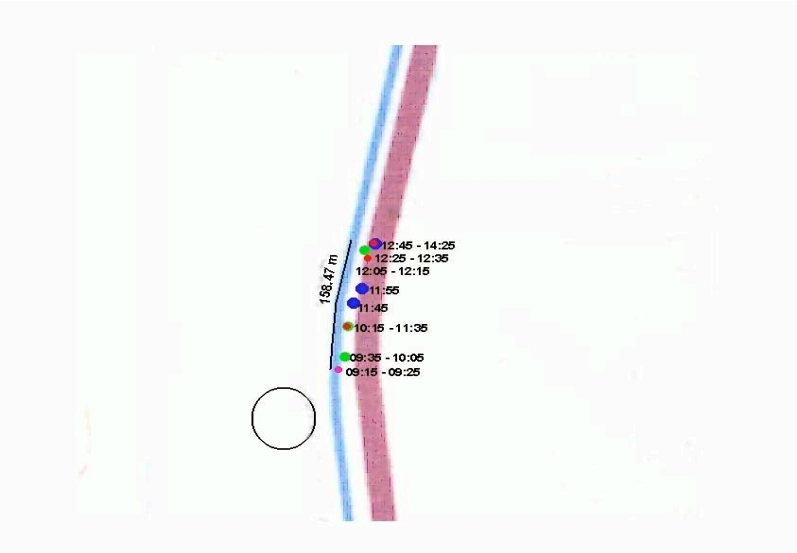


Figure 6.6: Daily movements of animal #17 in PSMIC adjacent farm dam on the 29/5/01. Circle indicates the position of farm dam 1.

Table 6.6: Areas where different behaviours were undertaken and their duration.

Behaviour	Time (mins)	Location
Basking	110	Banks of channel
Swimming	30	Channel
Walking	170	Banks of channel

Daily Movements: Included a section of irrigation channel of length 158 m and area 1580 m². Individual remained within the irrigation channel throughout the day. Distance moved 179 m equating to a speed of 0.58 m min^{-1}. No burrow locations observed being used.

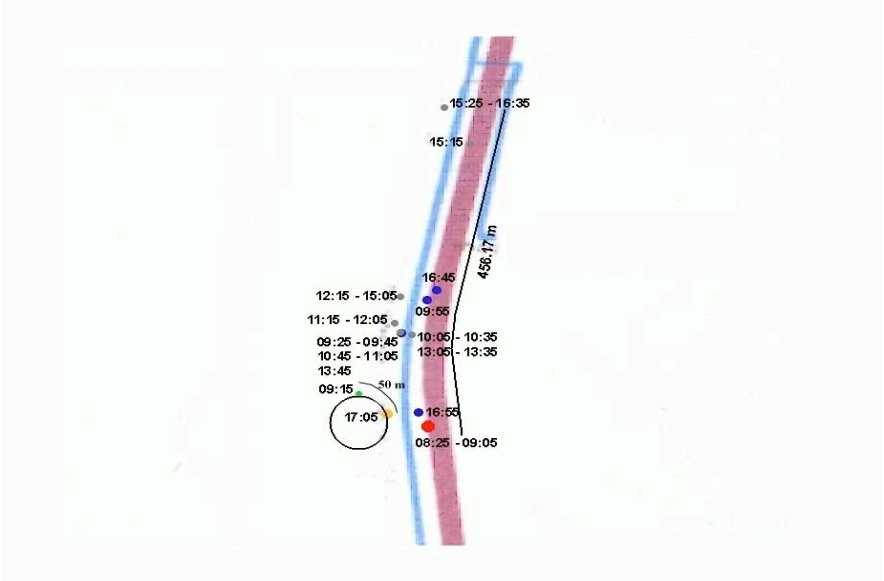


Figure 6.7: Daily movements of animal #17 in the PSMIC and farm dam 1 on the 5/2/02.

Table 6.7: Areas where different behaviours were undertaken and their duration.

Behaviour	Time (mins)	Location
Basking	50	Irrigation gateway
Swimming	50	Dam
Foraging (walking)	30	Channel benthos
Not seen	390	Channel

Daily Movements: Included a section of PSMIC of length 456 m and area 4560 m^2 and a 50 m length of farm dam bank of area 250 m^2. Individual moved from PSMIC to farm dam at 09:05 hrs and back to PSMIC at 11:05 hrs where it remained throughout the remainder of the day. Distance moved 1098 m equating to a speed of 2.11 m min^{-1}. One burrow location in the bank of the farm dam used upon retreat.

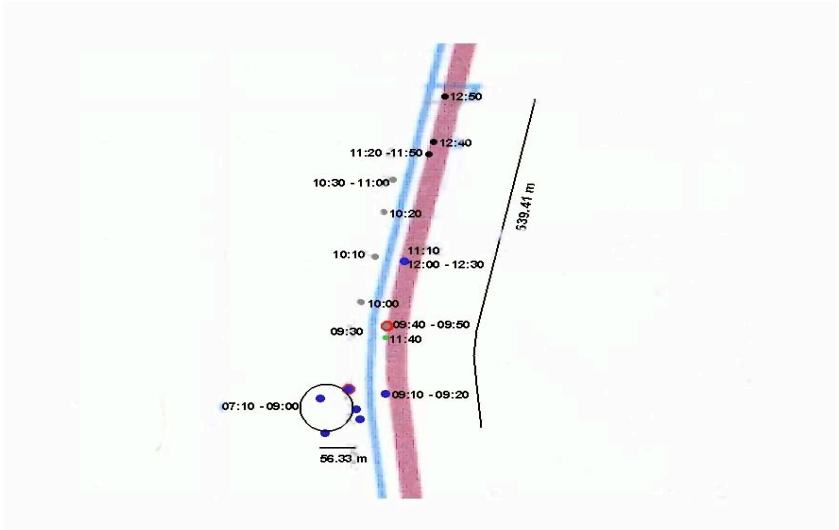


Figure 6.8: Daily movements of animal #17 in PSMIC and farm dam 1 on the 12/3/02.

Table 6.8: Areas where different behaviours were undertaken and their duration.

Behaviour	Time (mins)	Location
Basking	40	Banks of dam/ channel
Swimming	140	Dam/ channel
Foraging (walking)	50	Benthos / banks
Foraging (swimming)	30	Channel
Not seen	90	Channel

Daily Movements: Included a section of PSMIC of length 539 m and area 5390 m^2 and a large section of farm dam 1 with diameter 56 m and area 2463 m^2. Individual moved from dam to PSMIC at 08:10 hrs and was lost at 13:00 hrs. Distance moved 1318 m equating to a speed of 3.88 m min^{-1}. No burrow locations observed being used.

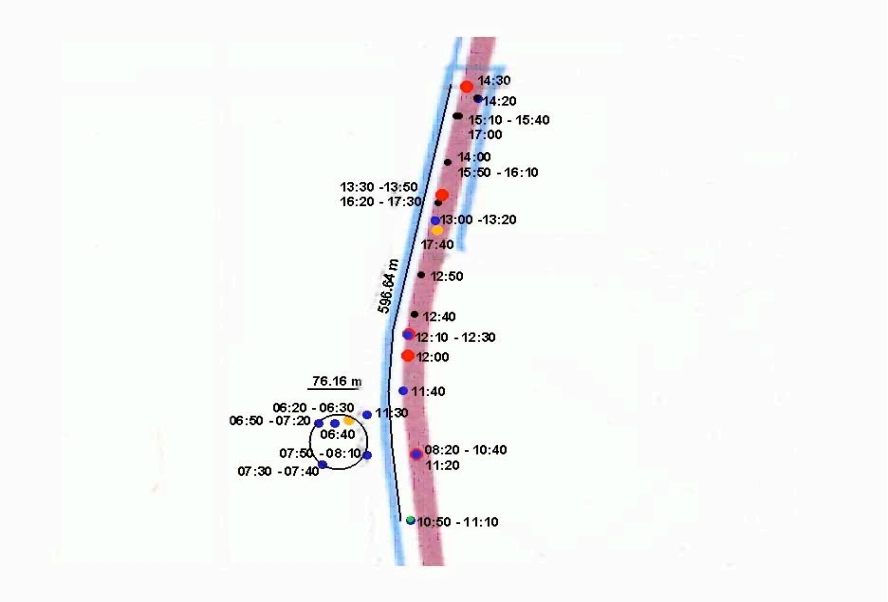


Figure 6.9: Daily movements of animal #17 in PSMIC and farm dam 1 on the 19/4/02.

Table 6.9: Areas where different behaviours were undertaken and their duration.

Behaviour	Time (mins)	Location
Basking	250	Banks of dam/ channel
Swimming	190	Dam/ channel
Foraging (walking)	30	Benthos / banks
Foraging (swimming)	170	Channel / dam

Daily Movements: Included a section of PSMIC of length 596 m and area 5960 m² and all of farm dam 1 with a diameter 76 m and area 4536 m². Individual moved from farm dam to PSMIC at 08:10 hrs. Distance moved 1206 m equating to a speed of 1.83 m min^{-1}. One burrow in bank of the farm dam used before emergence and one in bank of channel used after retreat.

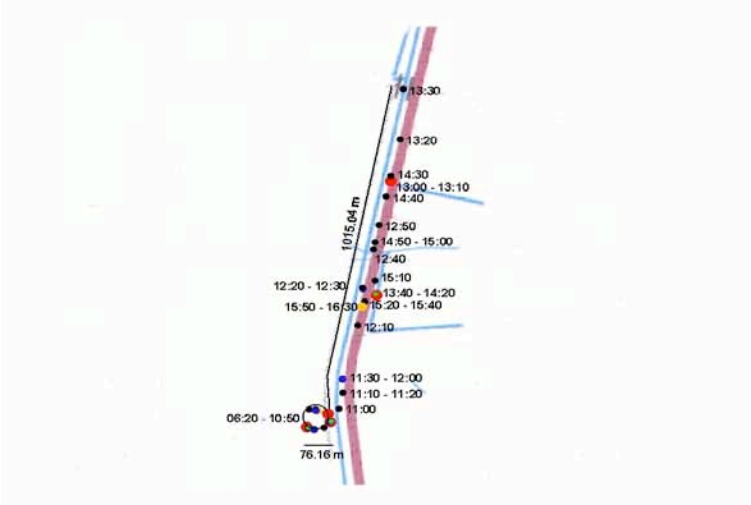


Figure 6.10: Daily movements of animal #17 in PSMIC and farm dam 1 on the 23/4/02.

Table 6.10: Areas where different behaviours were undertaken and their duration.

Behaviour	Time (mins)	Location
Basking	100	Banks of dam/ channel
Swimming	100	Dam/ channel
Foraging (walking)	40	Banks of dam/channel/access road
Foraging (swimming)	270	Channel / dam
Walking	10	Banks of channel/access road

Daily Movements: Included a section of PSMIC of length 1015 m and area 10150 m² and all of farm dam 1 with diameter 76 m and area 4536 m². Individual moved from farm dam to PSMIC at 11:00 hrs where it remained throughout the remainder of the day before retreating to a burrow at 15:50 where it remained until the observation day was terminated at 16:30 hrs. Distance moved 2758 m equating to a speed of 4.84 m min^{-1}. One burrow in bank of PSMIC used upon retreat and one burrow in bank of the farm dam used before emergence.

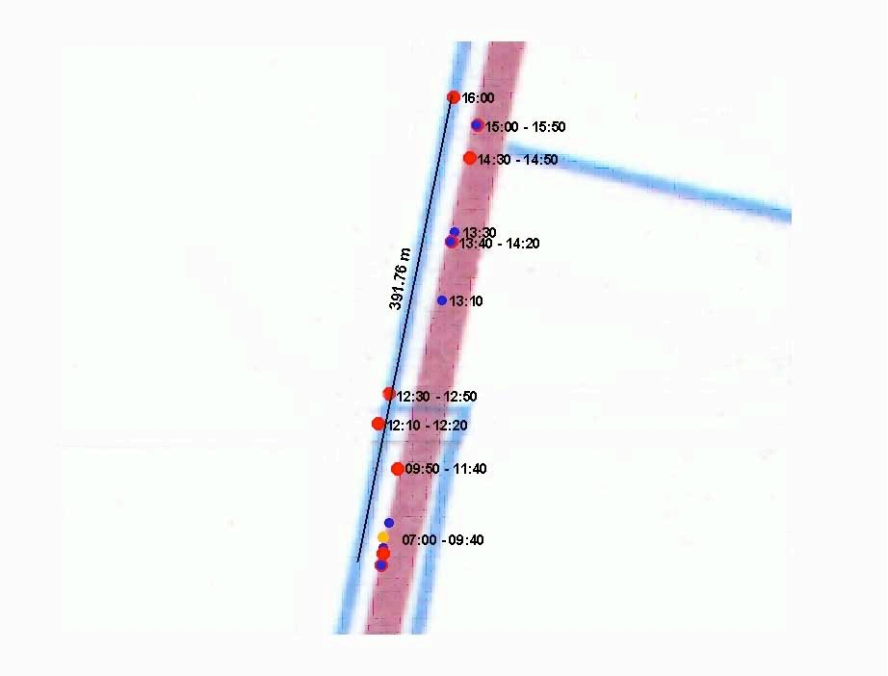


Figure 6.11: Daily movements of animal #17 in the PSMIC on the 21/5/02.

Table 6.11: Areas where different behaviours were undertaken and their duration.

Behaviour	Time (mins)	Location
Basking	310	Banks of dam/ channel
Swimming	160	Dam/ channel

Daily Movements: Included a section of PSMIC of length 391 m and area 3910 m². Individual remained within irrigation channel throughout the day. Distance moved 530 m equating to a speed of 0.77 m min^{-1}. One burrow in the bank of the PSMIC used before emergence.

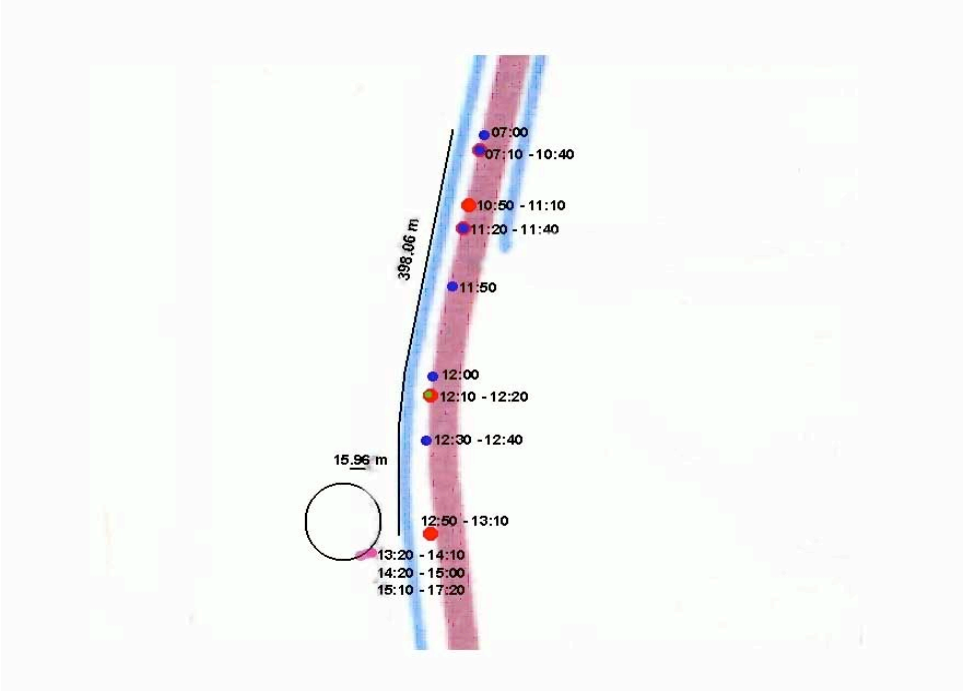


Figure 6.12: Daily movements of animal #17 in PSMIC and farm dam 1 on the 18/6/02.

Table 6.12: Areas where different behaviours were undertaken and their duration.

Behaviour	Time (mins)	Location
Basking	140	Banks of dam/ channel
Swimming/floating on weed	230	Dam/ channel

Daily Movements: Included a section of PSMIC of length 398 m and area 3980 m² and a small section of farm dam 1 with diameter 15 m and area 176 m². Individual moved from PSMIC to farm dam at 13:10hrs where it remained throughout the remainder of the day. Distance moved 477 m equating to a speed of 0.78 m min^{-1}. No burrow locations observed being used.

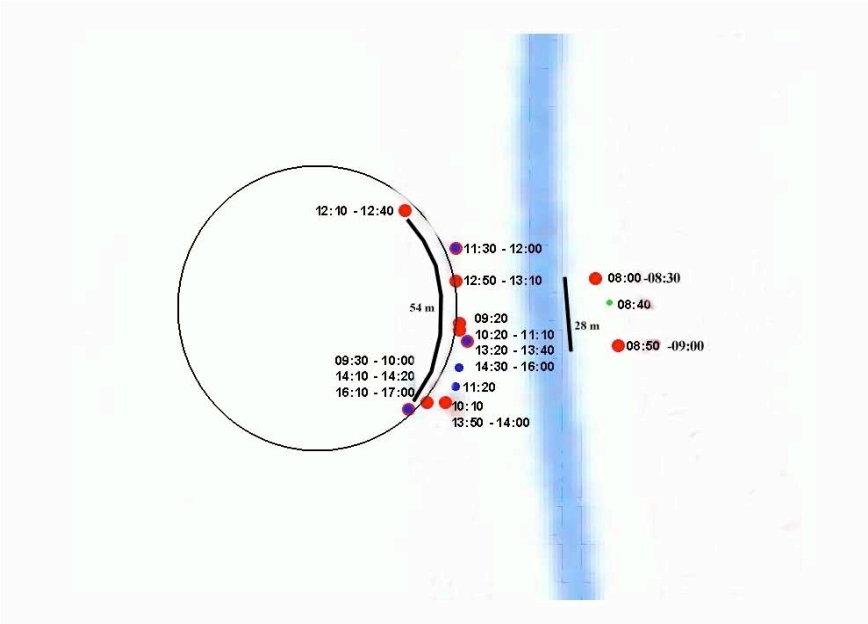


Figure 6.13: Daily movements of animal #17 in PSMIC and farm dam 1 on the 23/7/02.

Table 6.13: Areas where different behaviours were undertaken and their duration.

Behaviour	Time (mins)	Location
Basking	390	Banks of dam/ channel
Swimming	150	Dam/ channel
Walking	10	Banks of channel

Daily Movements: Included a section of PSMIC of length 28 m and area 280 m² and a length of bank on the eastern edge of farm dam 1 with length 54 m and area 270 m². Individual moved from PSMIC to farm dam at 09:00 hrs where it remained throughout the remainder of the day. Distance moved 310 m equating to a speed of 0.57 m min^{-1}. No burrow locations observed being used.

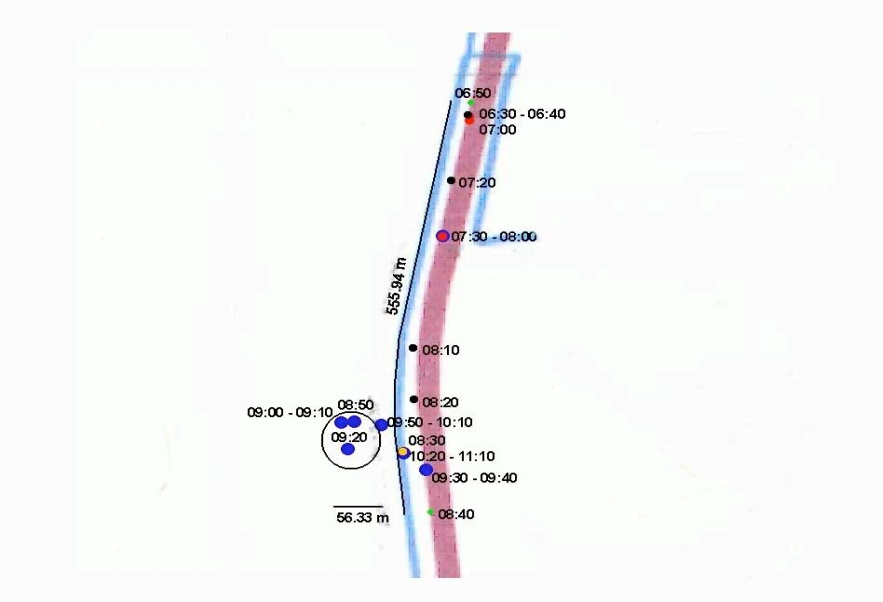
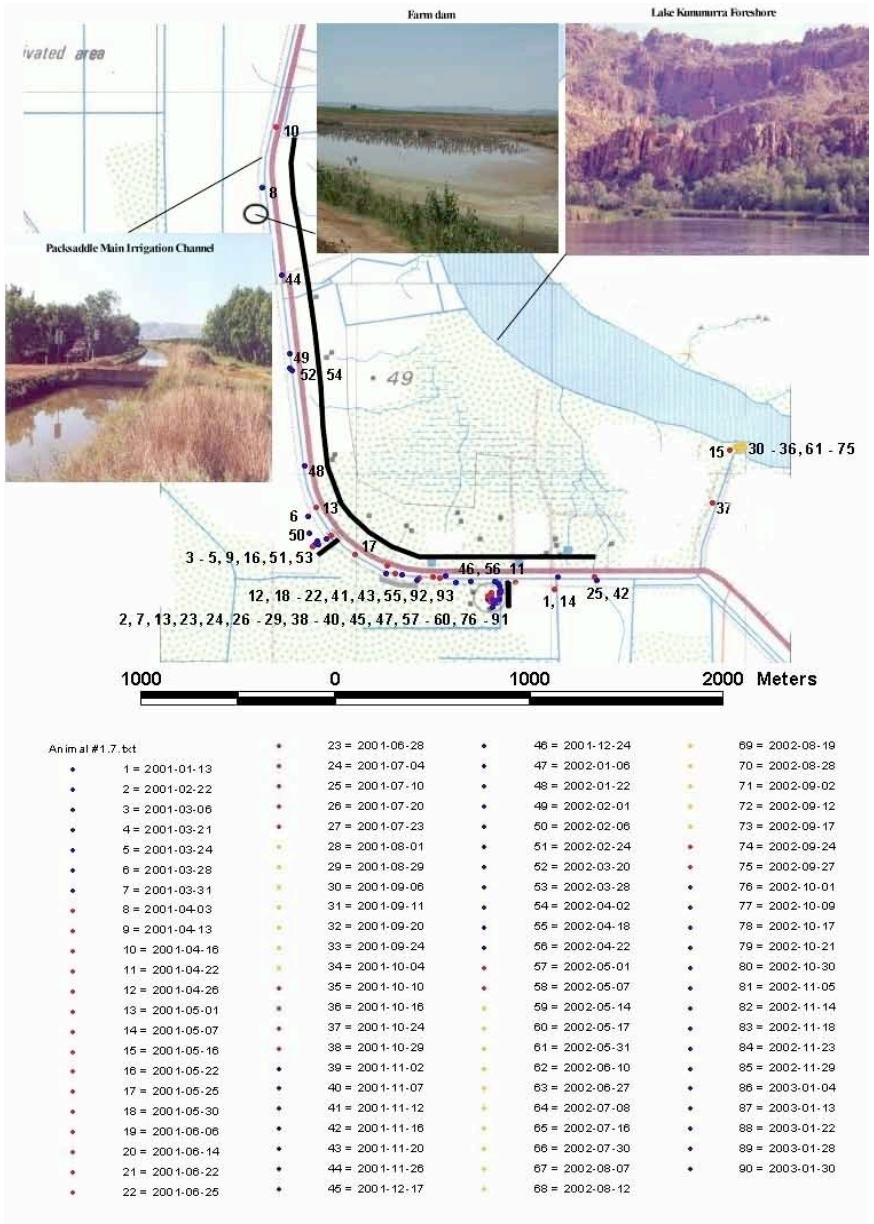


Figure 6.14: Daily movements of animal #17 in PSMIC and farm dam 1 on the 23/11/02.

Table 6.14: Areas where different behaviours were undertaken and their duration.

Behaviour	Time (mins)	Location
Basking	60	Banks of dam/ channel
Swimming	140	Dam/ channel
Foraging (walking)	20	Banks of dam/channel/access road
Foraging (swimming)	40	Channel / dam

Daily Movements: Included a section of PSMIC of length 555 m and area 5550 m² and a large section of farm dam 1 with diameter 56 m and area 2463 m². Individual moved from PSMIC to dam at 08:20 and then back to PSMIC at 10:20hrs where it remained throughout the remainder of the day. Distance moved 1072 m equating to a speed of 3.83 m min^{-1}. One burrow in the bank of PSMIC used before emergence.



Animal #1.7

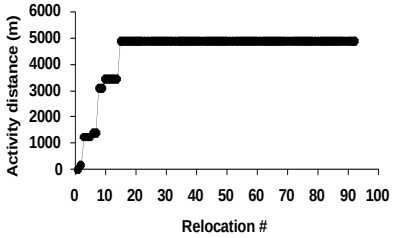


Figure 6.15: Left: Long-term movements of animal #1.7 (SVL = 430 mm, Sex = UC) in the PSMIC, black circle indicates the position of farm dam 1 and grey circle farm dam 2 adjacent the PSMIC. Areas used during all daily observations also indicated (grey). Above: activity distance accumulated after each subsequent positional fix following release.

Table 6.15: Length, width and area of total activity areas and core activity areas (CAA).

Site	Total Length (m)	Width (m)	Area (m^2)	CAA length (m)	Width (m)	Area (m^2)
Channel	4870	10	48700	3373	10	33730
Farm dam	60		2827	60		2827
Drain	60	5	300	60	5	300

Long-term movements: Animal #1.7 used three core activity areas a length of the PSMIC, a farm dam adjacent the PSMIC and a length of irrigation drain. It was only found outside these areas on; 3/4/01, 15/4/01, 16/5/01, 24/10/01, 26/11/01, 22/1/02 – 1/2/02, 20/3/02, 2/4/02. Two notable movements away from these areas included moving to the junction of the PSMIC and Lake Kununurra (LK) burrowing and becoming inactive. Inactivity at this site occurred in two consecutive years between the 6/9/01 – 16/10/01 and 31/5/02 – 27/9/02.

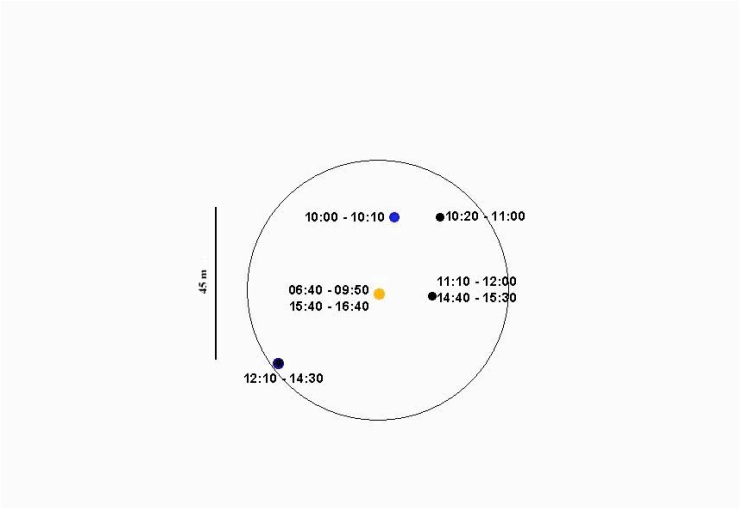


Figure 6.16: Daily movements of animal #1.7 in farm dam 2 on the 29/1/03.

Table 6.16: Areas where different behaviours were undertaken and their duration.

Behaviour	Time (mins)	Location
Swimming	120	In dam
Foraging (swimming)	220	In dam

Daily movements: Included a large section of farm dam 2 with diameter 45 m and area 1590 m². Individual remained in farm dam throughout day until retreating to a burrow at 15:40 hrs where it remained until the observation day was terminated at 16:40 hrs. Distance moved 324 m equating to a speed of 0.95 m min^{-1}. One burrow location used both before emergence and on retreat in the bank of the farm dam.

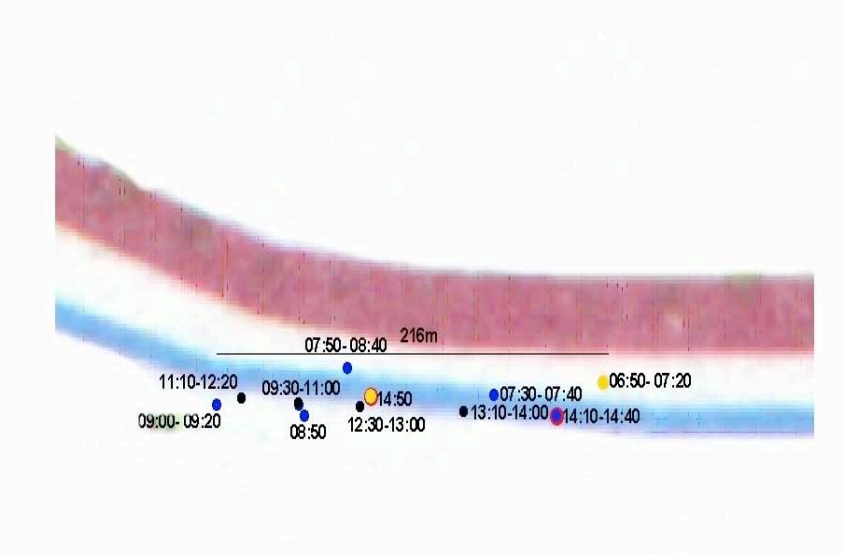


Figure 6.17: Daily movements of animal #1.7 in PSMIC on the 31/1/03.

Table 6.17: Areas where different behaviours were undertaken and their duration.

Behaviour	Time (mins)	Location
Basking	20	Banks of channel
Swimming	270	Channel
Foraging (swimming)	190	Channel

Daily Movements: Included a section of the PSMIC length 216 m and area 2160 m². Individual remained in channel throughout the day. Distance moved 556m equating to a speed of 1.16 m min^{-1}. Two different burrows within the bank of the PSMIC used before emergence and upon retreat.

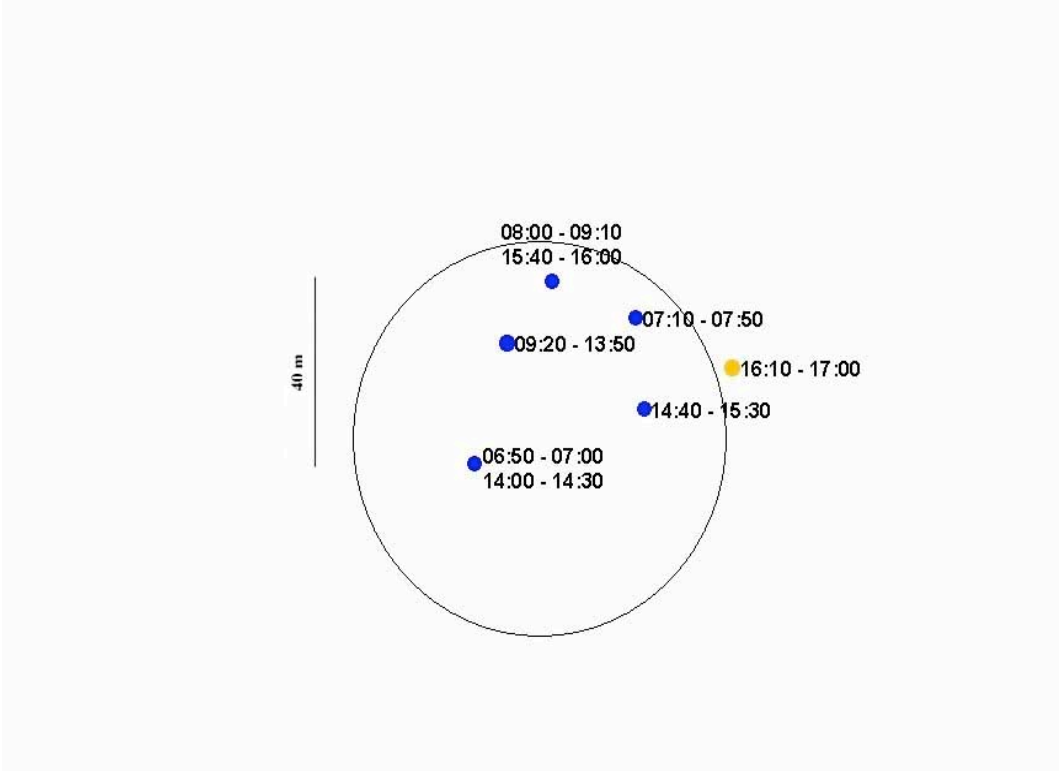
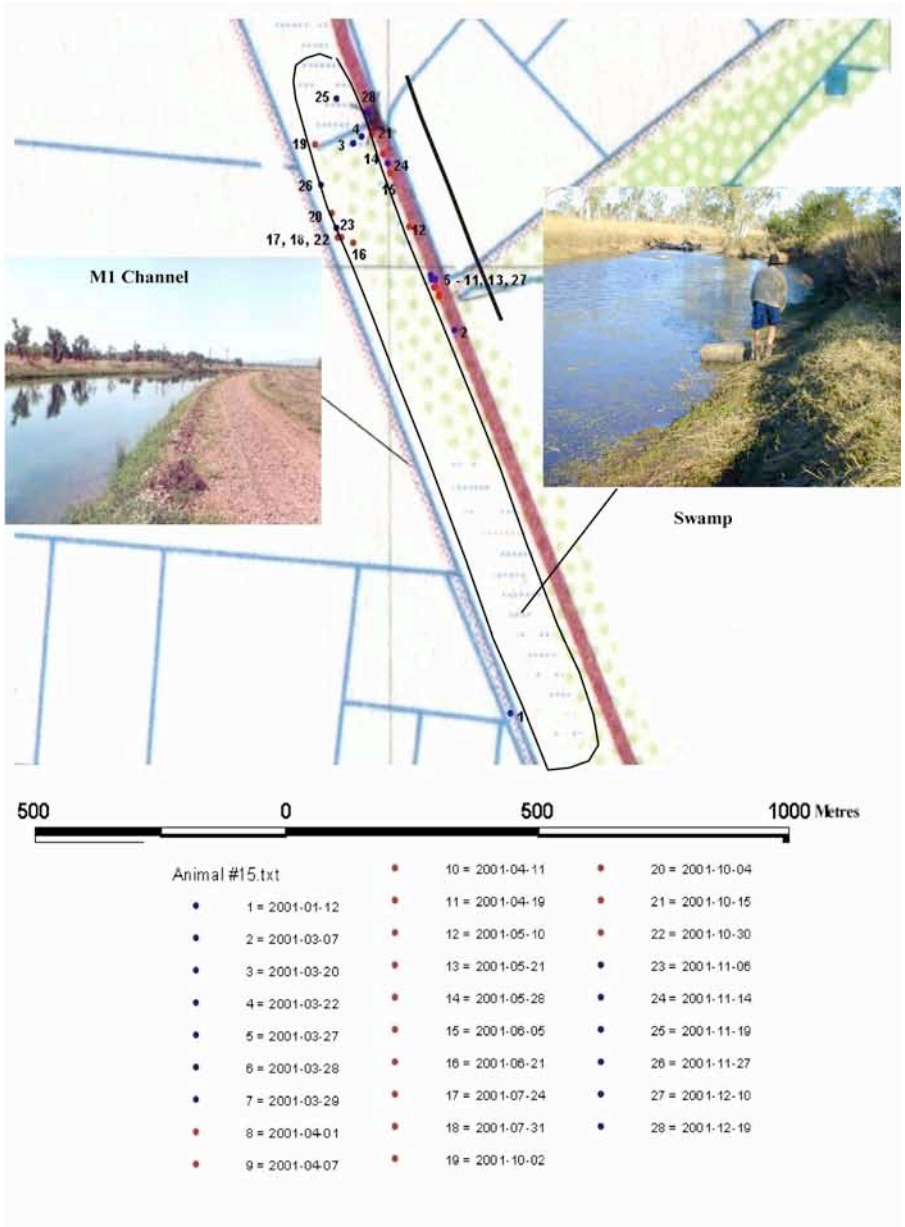


Figure 6.18: Left: Daily movements of animal #1.7 in farm dam 2 on the 2/2/03.

Table 6.18: Areas where different behaviours were undertaken and their duration.

Behaviour	Time (mins)	Location
Swimming	570	In dam

Daily Movements: Included a section of the farm dam diameter 40 m and area 1256 m². Individual remained in dam throughout the day until it retreated into a burrow at 16:10 hrs where it remained until the observation day was terminated at 17:00 hrs. Distance moved 399 m equating to a mean speed of 0.7 m min^{-1}. One burrow location in bank of farm dam used upon retreat.



Animal #15

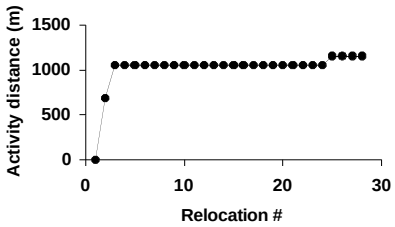
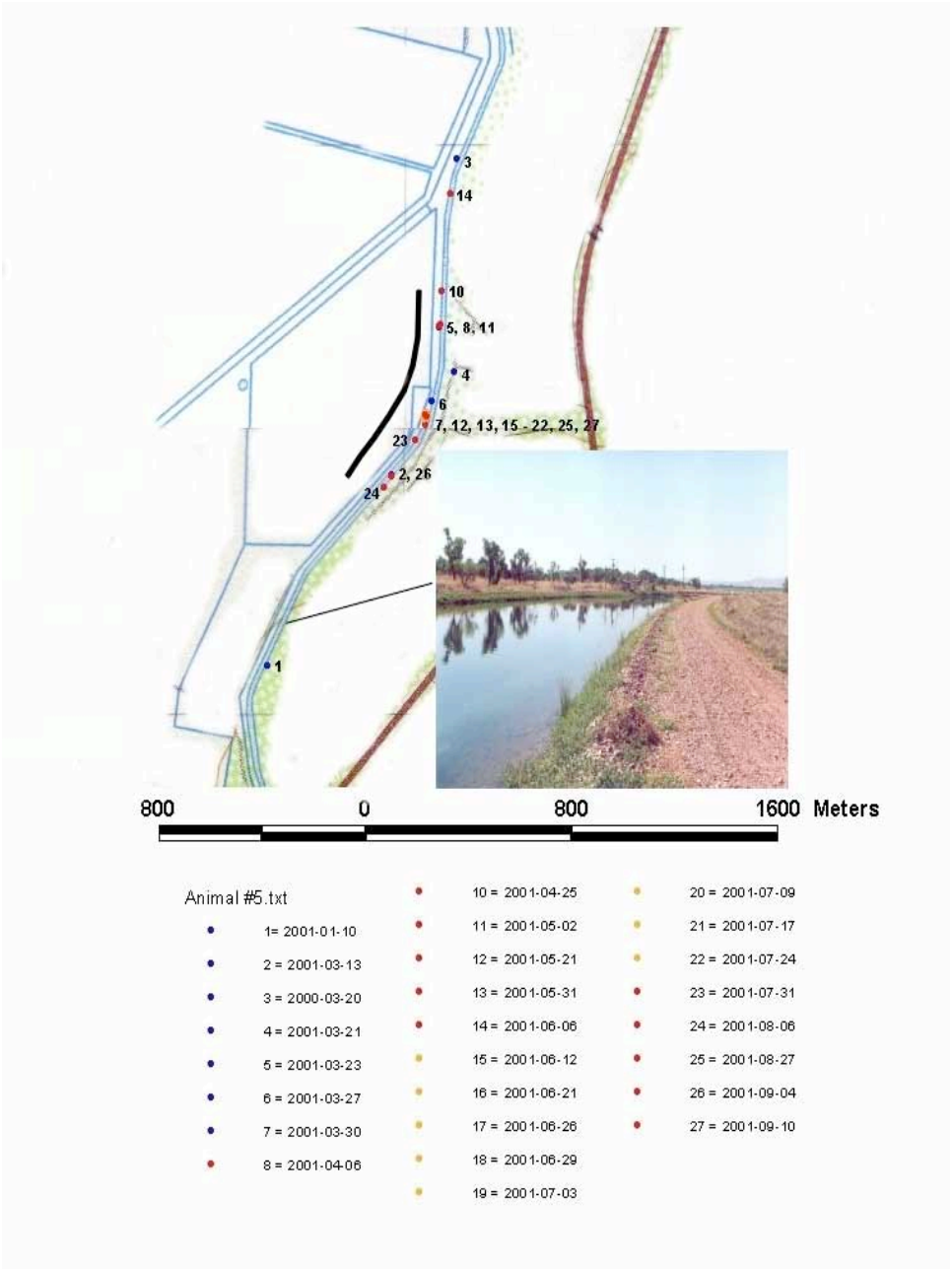


Figure 6.19: Left: Long-term movements of animal #15 (SVL = 430 mm, Sex = UC) in Ivanhoe Plains Main Irrigation Channel (IPM1) and a swamp adjacent the IPM1, outline indicates position of a seasonal (wet season) swamp adjacent IPM1. Above: Activity distance accumulated after each subsequent positional fix following release.

Table 6.19: Length, width and area of total activity areas and core activity areas (CAA).

Site	Total Length (m)	Width (m)	Area (m^2)	CAA length (m)	Width (m)	Area (m^2)
Channel + swamp	1152	100	115200	460	100	46000

Long-term movements: Animal #15 used one core activity area a length of the combined IPM1 and swamp. It remained exclusively within this core activity area only being found outside this area upon capture and release on the 12/1/01. Animal #15 regularly moved between IPM1 and the swamp. Animal # 15 was not found after the 19/12/01.



Animal #5

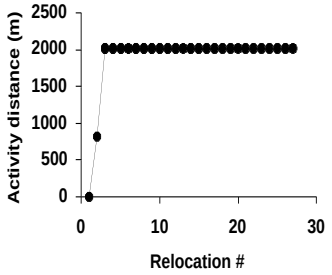
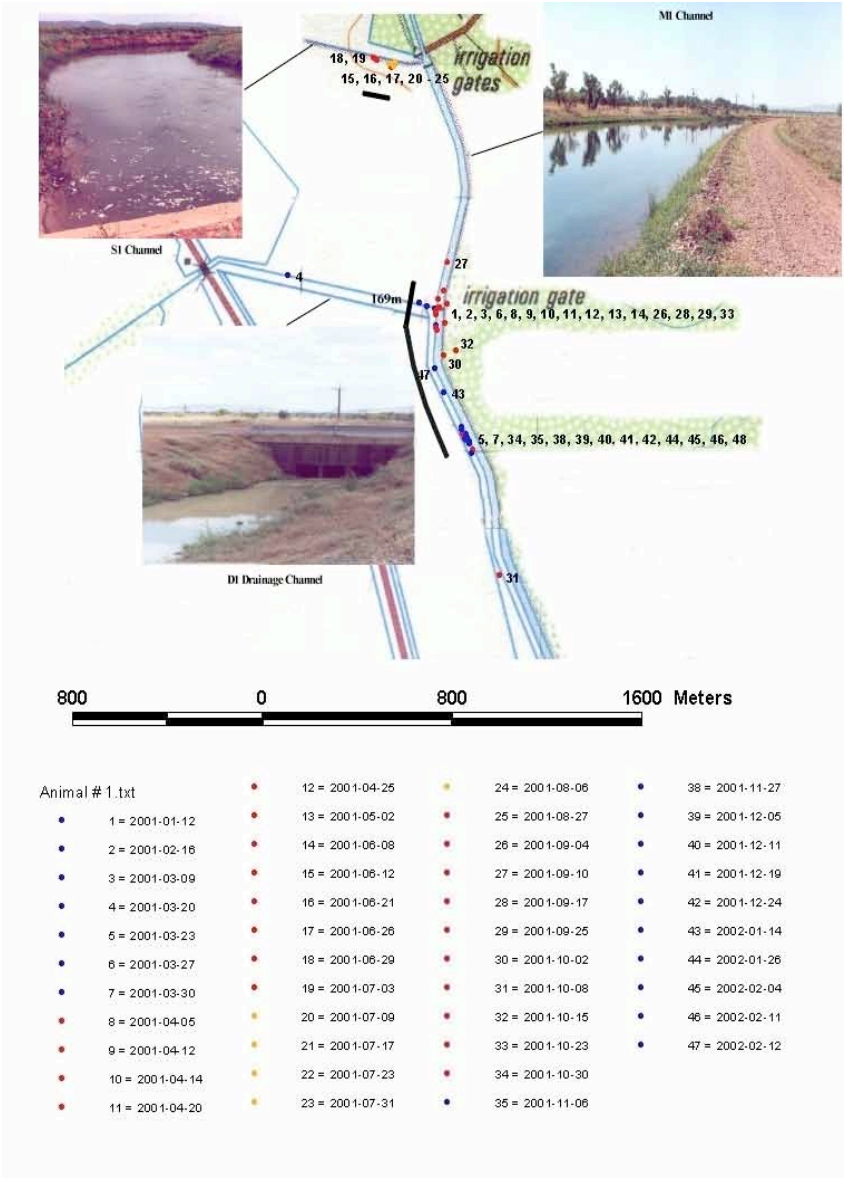


Figure 6.20: Left: Long-term movements of animal #5 (SVL = 470 mm, Sex = UC) in the IPM1. Above: Activity distance accumulated after each subsequent positional fix following release.

Table 6.20: Length, width and area of total activity areas and core activity areas (CAA).

Site	Total Length (m)	Width (m)	Area (m^2)	CAA length (m)	Width (m)	Area (m^2)
Channel	2014	20	40280	708	20	14160

Long-term movements: Animal #5 used a length of the IPM1. It used one core activity area a length of IPM1. It was only found outside this area upon capture and release on the 10/1/01 and subsequently on the 20/3/01 and the 6/6/01. Animal #5 burrowed and became inactive within its core activity area between the 12/6/01 – 24/7/01. Animal # 5 was not found after the 10/9/01.



Animal #1

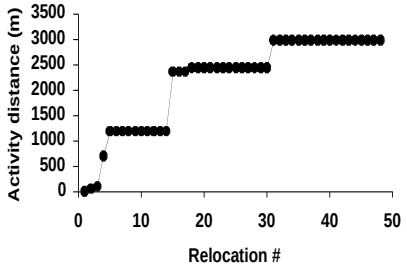
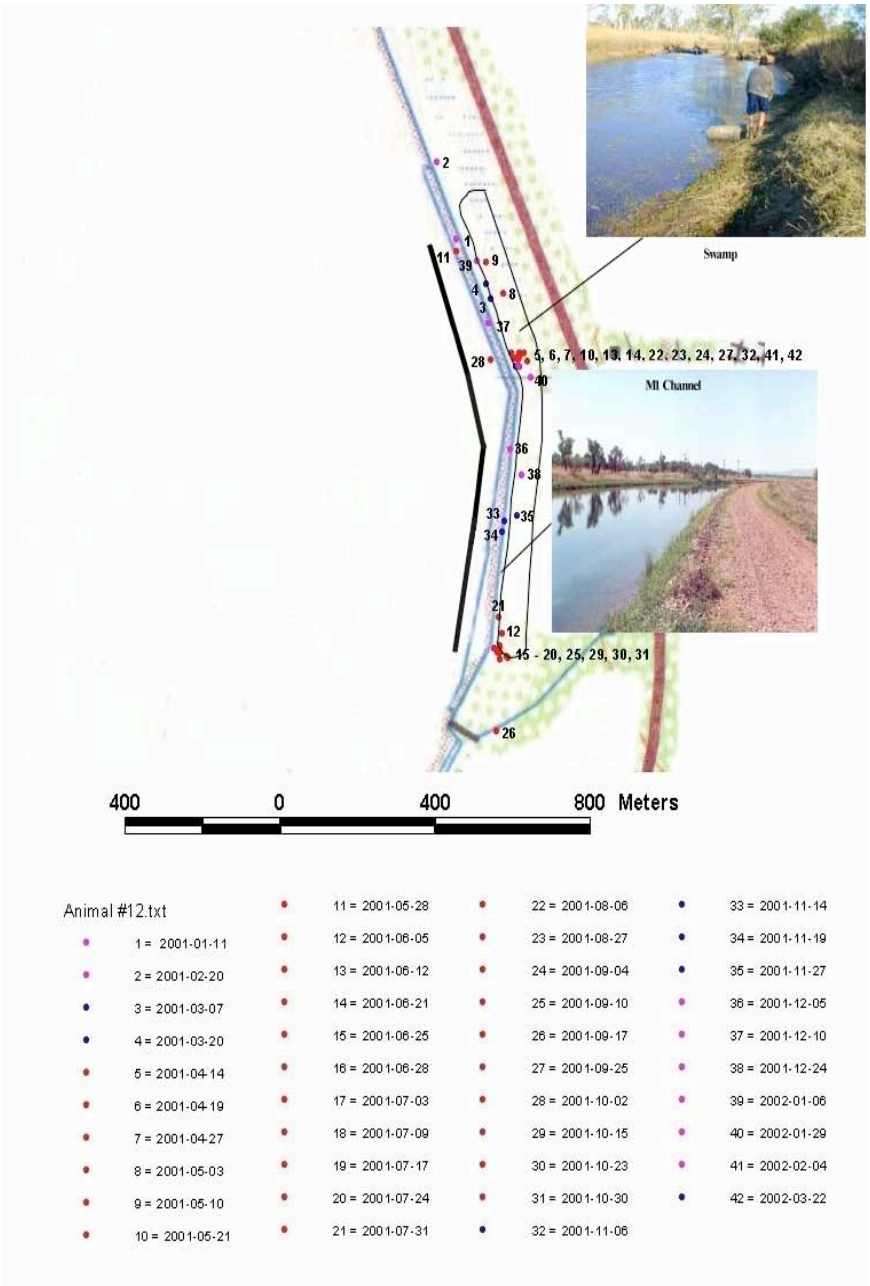


Figure 6.21: Left: Long-term movements of animal #1 (SVL = 535 mm, Sex = UC) in the IPM1, Supply Channel (S1) and Drainage Channel (D1). Above: Activity distance accumulated after each subsequent positional fix following release.

Table 6.21: Length, width and area of total activity areas and core activity areas (CAA).

Site	Total Length (m)	Width (m)	Area (m^2)	CAA length (m)	Width (m)	Area (m^2)
Channel	2978	20	59560	110	10	1100
Channel				710	20	14200

Long-term movements: Animal #1 used a length of IPM1, S1 and D1. It used two core activity areas one a length of IPM1channel and a length of S1 Channel. It remained in its IPM1 areas between the 12/1/01 – 12/6/01 before moving to its S1 area and again returning to its IPM1 area on the 17/9/01. It was only found outside these two core activity areas soon after release on the 20/3/01 and between the 2/10/01 – 15/10/01 and the 14/1/02 – 12/2/02. Animal #1 burrowed and became inactive within its S1 area between the 9/7/01 – 6/8/01. Animal #1 was not found after the 12/2/02.



Animal #12

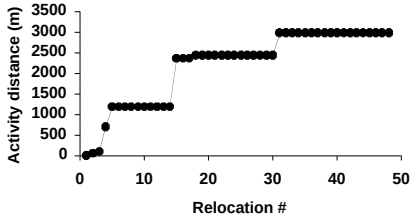
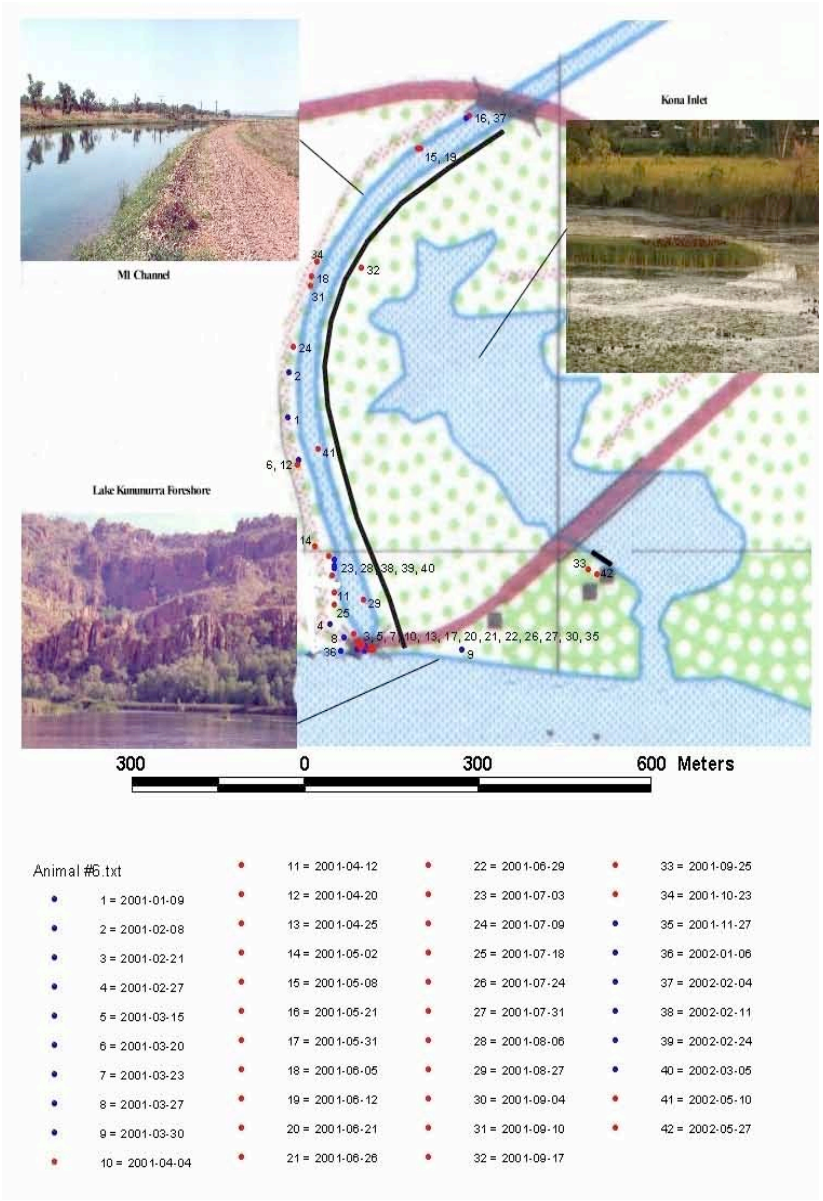


Figure 6.22: Left: Long-term movements of animal #12 (SVL = 390 mm, Sex = UC) in the IPM1 and swamp adjacent IPM1, outline indicates position of seasonal (wet season) swamp adjacent IPM1. Above: Activity distance accumulated after each subsequent positional fix following release.

Table 6.22: Length, width and area of total activity areas and core activity areas (CAA).

Site	Total Length (m)	Width (m)	Area (m^2)	CAA length (m)	Width (m)	Area (m^2)
Channel + swamp	1412	50	70600	950	50	47500

Long-term movements: Animal #12 used a length of the combined IPM1 and adjacent swamp. It used one core activity areas a length of the combined IPM1 and swamp. It regularly moved between the northern and southern end of its core activity area. It was only found outside this area soon after release on the 20/2/01 and subsequently on the 17/9/01. Animal #12 was not found after the 22/3/02.



Animal #6

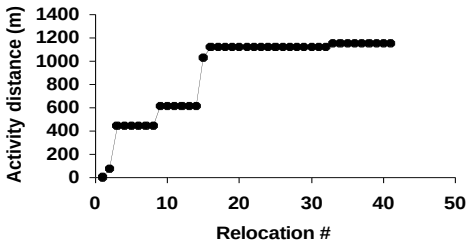
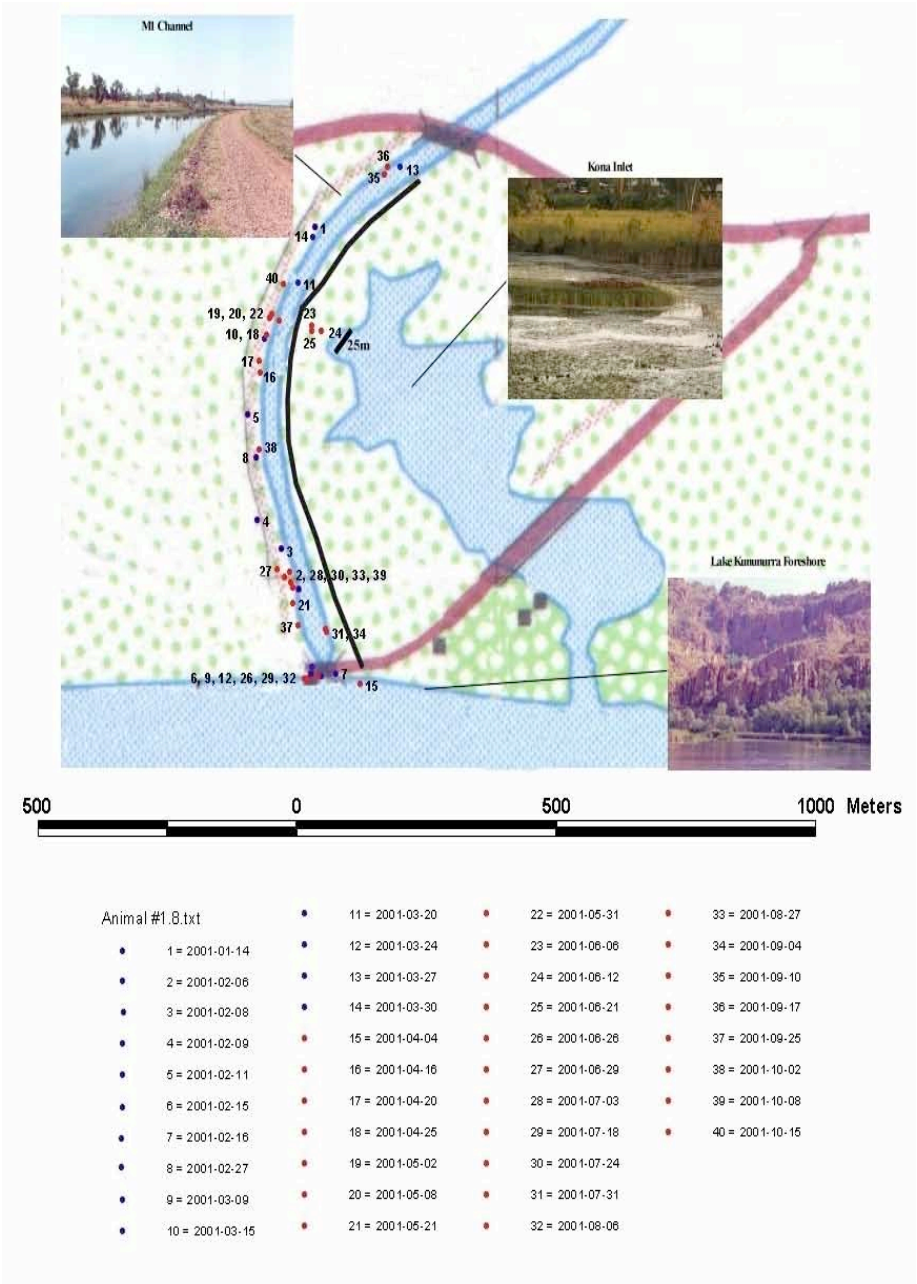


Figure 6.23: Left: Long-term movements of animal #6 (SVL = 390 mm, Sex = UC) in the IPM1, LKF and Kona Inlet (KI). Above: Activity distance accumulated after each subsequent positional fix following release.

Table 6.23: Length, width and area of total activity areas and core activity areas (CAA).

Site	Total Length (m)	Width (m)	Area (m^2)	CAA length (m)	Width (m)	Area (m^2)
Channel	1006	20	20137	950	20	19000
Kona inlet	28	10	280	30	10	300

Long-term movements: Animal #6 used a length of IPM1 and KI. It used two core activity areas one a length of the IPM1 and a second a length of KI. It remained in its IPM1 core activity area only moving briefly to its KI area on two occasions in consecutive years, being found there on the 25/9/01 and the 27/5/02. Animal #6 was not found after the 27/5/02.



Animal #1.8

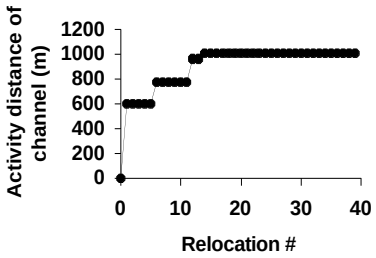
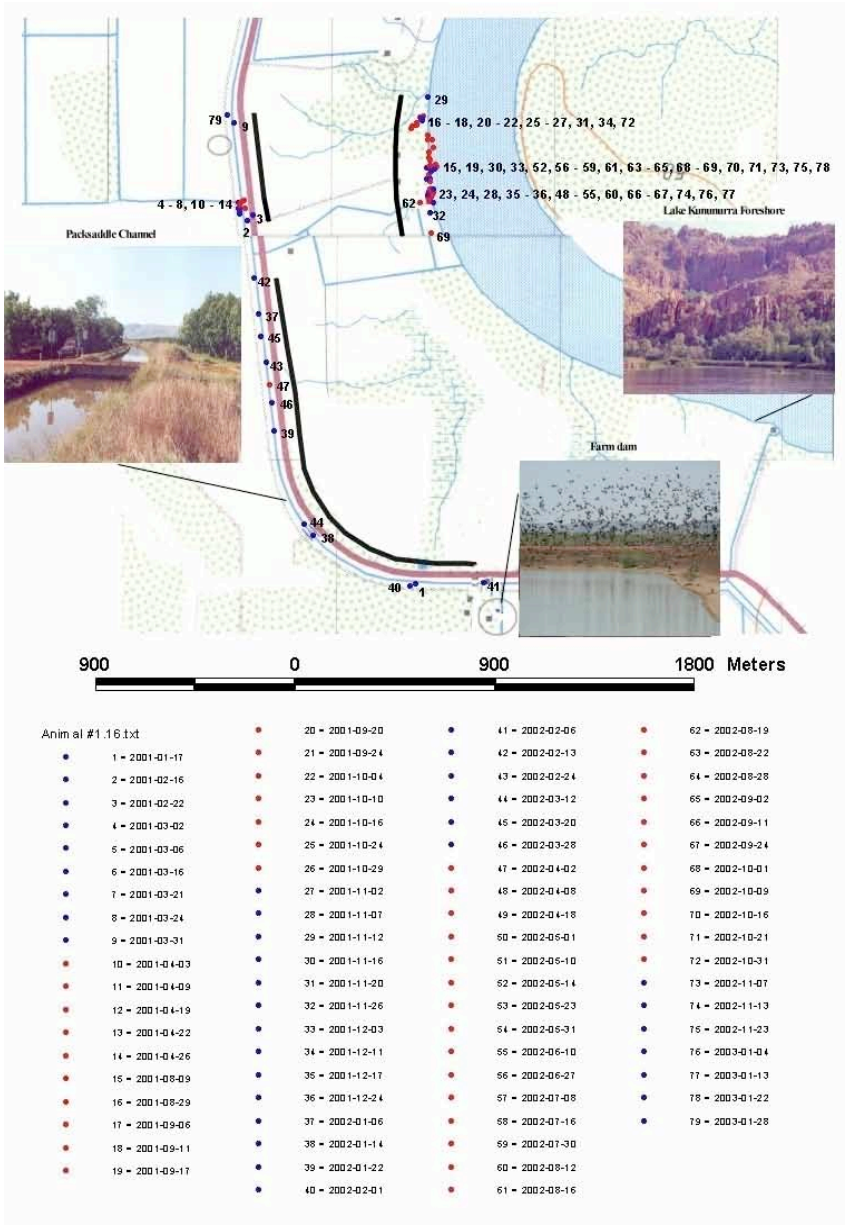


Figure 6.24: Left: Long-term movements of animal #1.8 (SVL = 420 mm, Sex = UC) in the IPM1, LKF and KI. Above: Activity distance accumulated after each subsequent positional fix following release.

Table 6.24: Length, width and area of total activity areas and core activity areas (CAA).

Site	Total Length (m)	Width (m)	Area (m^2)	CAA length (m)	Width (m)	Area (m^2)
Channel	1006	20	20137	905	20	18100
Kona inlet	25	10	250	25	10	250

Long-term movements: Animal #1.8 used a length of IPM1 and KI. It used two core activity areas a length of the IPM1 and a length of KI. It remained in its IPM1 core activity area only moving to its KI area between the 6/6/01 – 21/6/01. Animal #1.8 was not found after the 15/10/01.



Animal #1.16

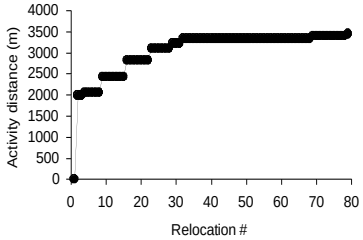
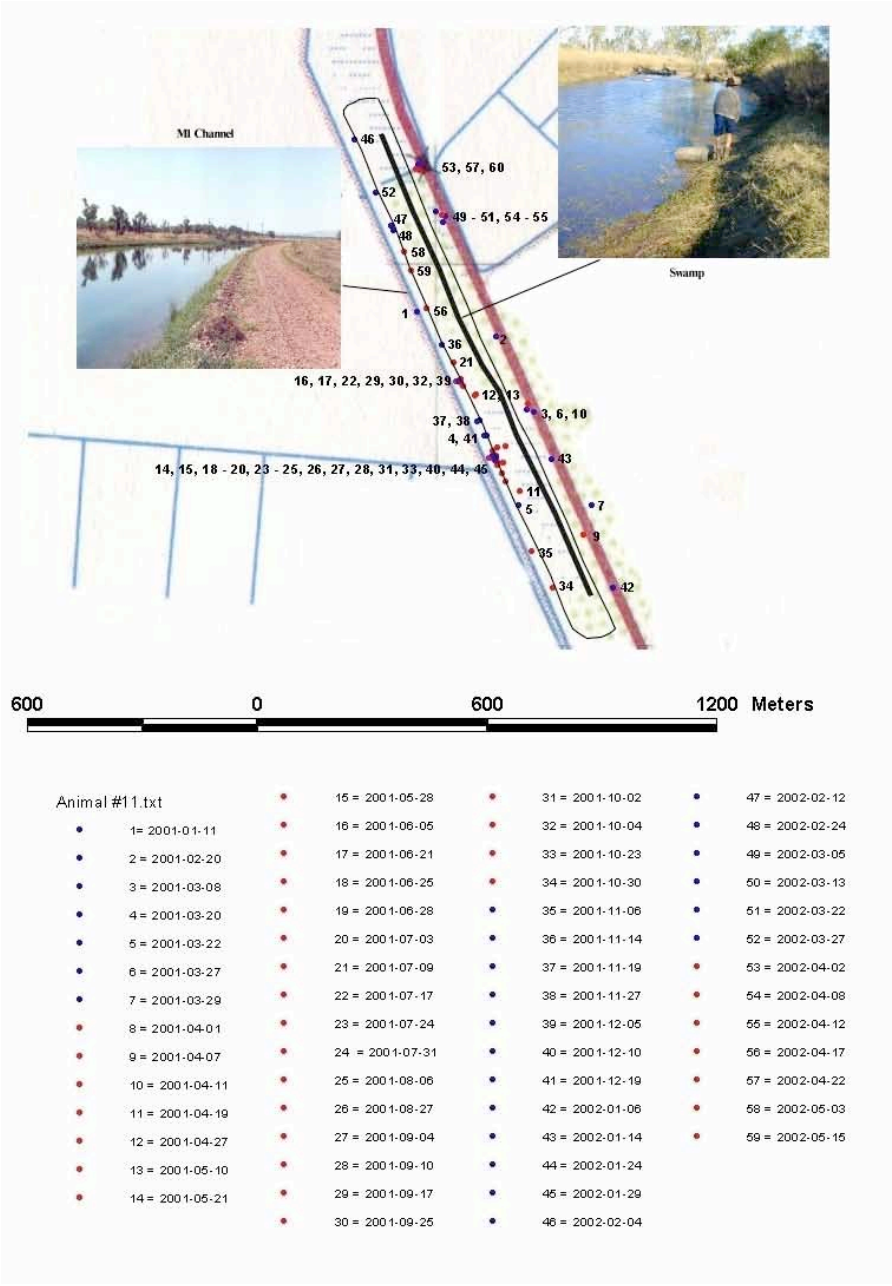


Figure 6.25: Left: Long-term movements of animal #1.16 (SVL = 450 mm, Sex = UC) in the PSMIC, LKF and a farm dam adjacent PSMIC, circles indicate the position of farm dams 1 and 2 adjacent the PSMIC. Above: Activity distance accumulated after each subsequent positional fix following release.

Table 6.25: Length, width and area of total activity areas and core activity areas (CAA).

Site	Total Length/diameter (m)	Width (m)	Area (m^2)	CAA length/diameter (m)	Width (m)	Area (m^2)
Channel	2815	10	28150	546	10	5460
				2312	10	23120
Foreshore	631	10	6310	631	10	6310

Long-term movements: Animal #1.16 used a length of PSMIC and LKF. It used three core activity areas two lengths of the PSMIC and a length of LKF. It remained in the PSMIC after release until moving to the LKF on the 9/8/01 where it remained until the 6/1/02. It then returned to the PSMIC before again moving back to the LKF on the 8/4/02. It remained in this area until moving back to the PSMIC area on the 28/1/03 where it remained until the completion of the study.



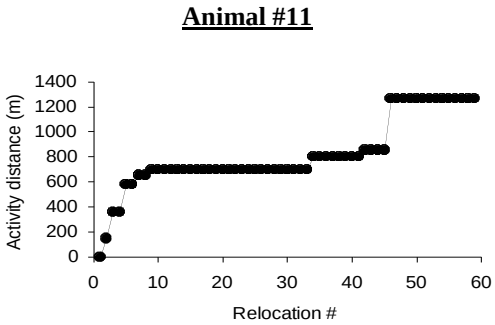
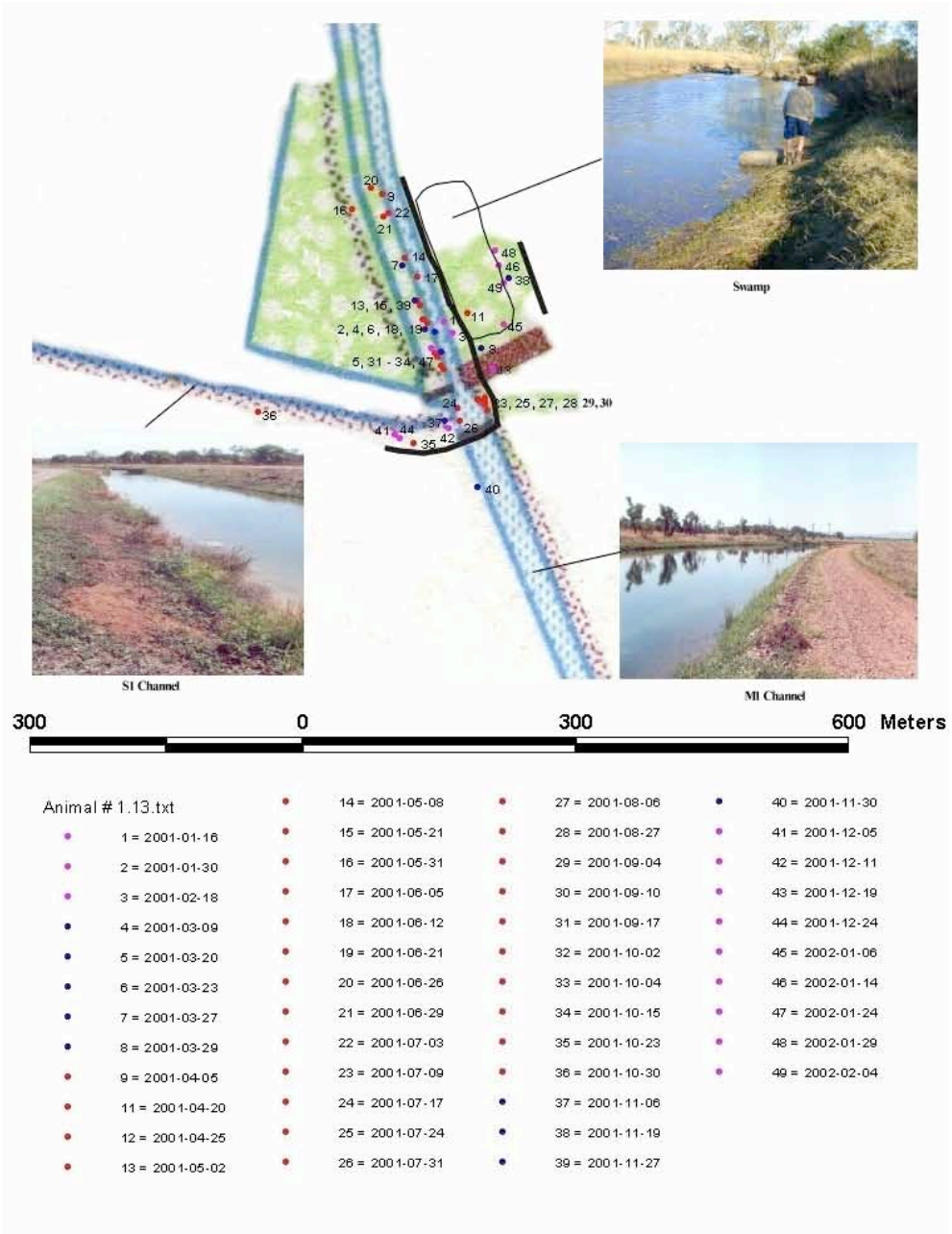


Figure 6.26: Left: Long-term movements of animal #11(SVL = 400 mm, Sex = UC) in the combined IPM1 and adjacent swamp, outline indicates the position of a seasonal (wet season) swamp adjacent the IPM1. Above: Activity distance accumulated after each subsequent positional fix following release.

Table 6.26: Length, width and area of total activity areas and core activity areas (CAA).

Site	Total Length (m)	Width (m)	Area (m^2)	CAA length (m)	Width (m)	Area (m^2)
Channel + swamp	1264	100	126400	1264	100	126400

Long-term movements: Animal #11 used a length of the combined IPM1 and swamp. It used one core activity area a length of the combined IPM1 and swamp. Animal #11 was not found after the 15/5/02.



Animal #1.13

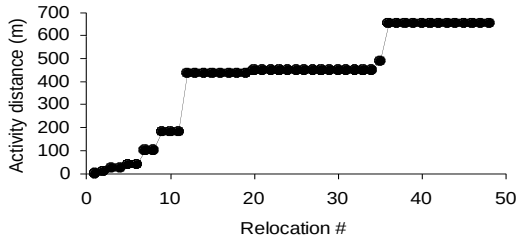
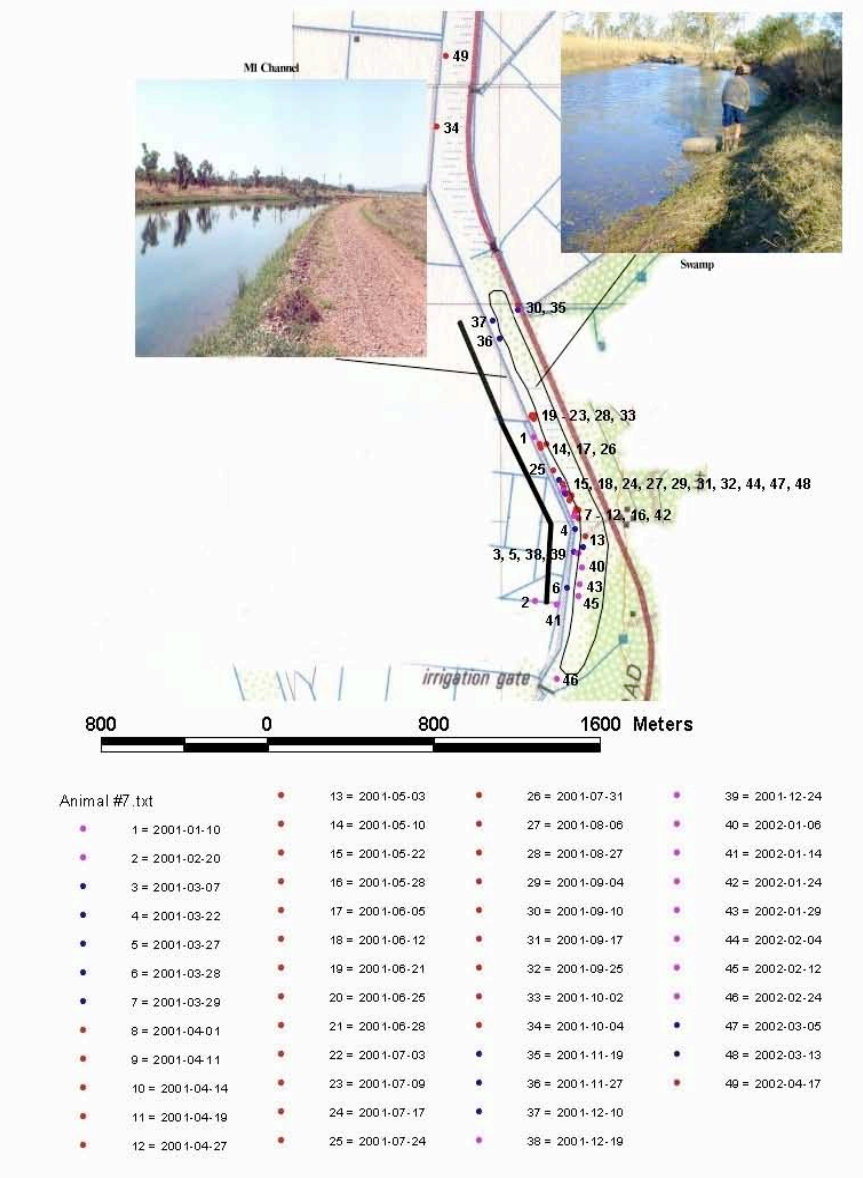


Figure 6.27: Left: Long-term movements of animal #1.13 (SVL = 420 mm, Sex = ♀) in the IPM1, S1 and swamp adjacent IPM1, outline indicates the position of a seasonal (wet season) swamp adjacent the IPM1. Above: Activity distance accumulated after each subsequent positional fix following release.

Table 6.27: Length, width and area of total activity areas and core activity areas (CAA).

Site	Total Length (m)	Width (m)	Area (m^2)	CAA length (m)	Width (m)	Area (m^2)
Channel	652	20	13040	356	20	7120
Swamp				82	50	4100

Long-term movements: Animal #1.13 used a length of both S1 and IPM1 and a swamp adjacent IPM1. It used two core activity areas a length of the IPM1 and S1 channels and a length of the swamp. It was only found outside these areas on the 30/10/01 and the 30/11/01. Fixes during mating season months show animal #1.13 moved into a swamp adjacent IPM1 in addition to moving west down S1 over the period 5/12/01 – 4/2/02. Animal #1.13 was not found after the 4/2/02.



Animal #7

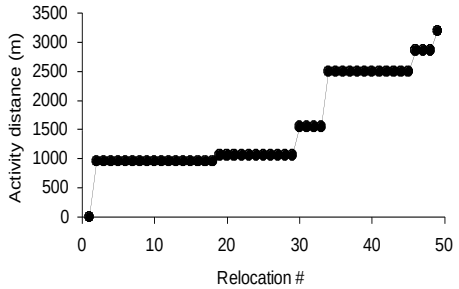
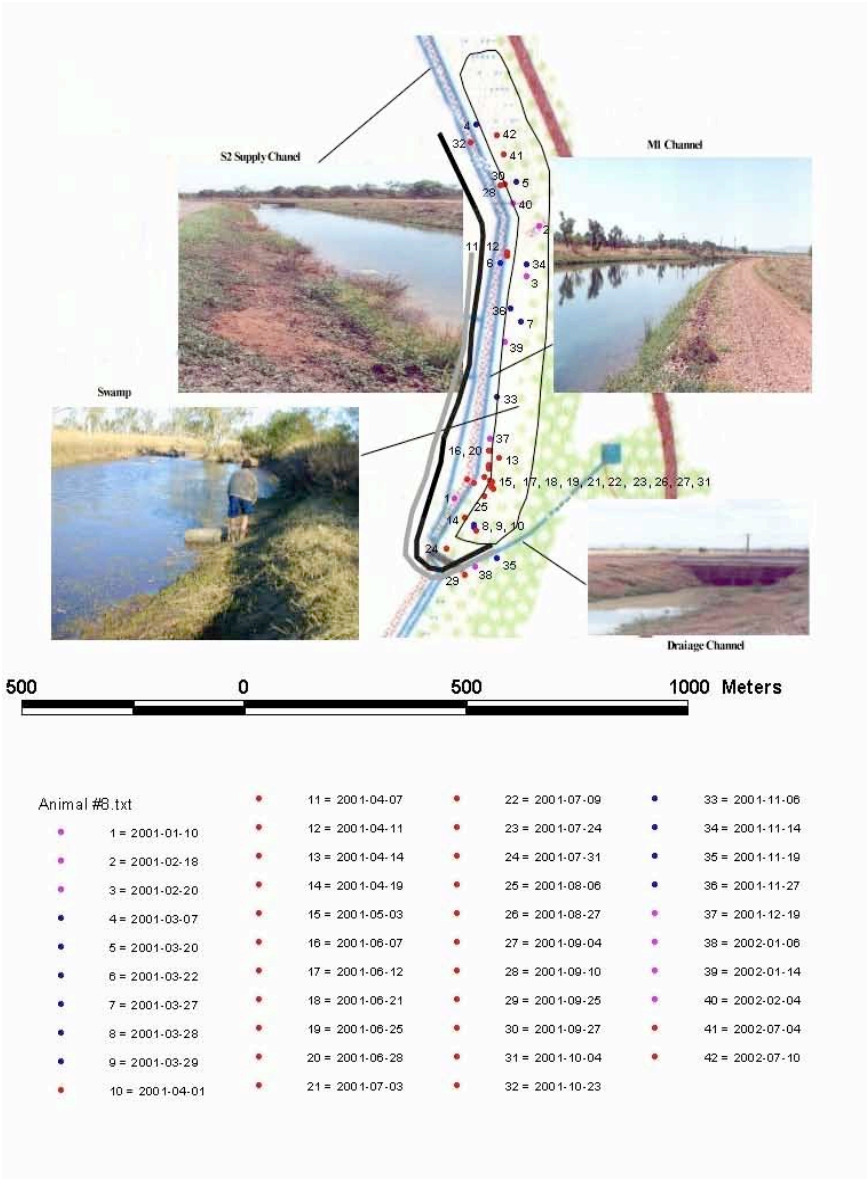


Figure 6.28: Left: Long-term movements of animal #7 (SVL = 470 mm, Sex = ♂) in the IPM1, S2 and adjacent swamp, outline indicates the position of a seasonal (wet season) swamp adjacent the IPM1. Above: Activity distance accumulated after each subsequent positional fix following release.

Table 6.28: Length, width and area of total activity areas and core activity areas (CAA).

Site	Total Length (m)	Width (m)	Area (m^2)	CAA length (m)	Width (m)	Area (m^2)
Channels + swamp	3186	100	318600	1375	100	136500

Long-term movements: Animal #7 used a length of the combined IPM1 and adjacent swamp. It used one core activity area a length of the combined IPM1 and swamp. It was only found outside this area on the 20/2/01 and the 24/2/02. Fixes during mating season months show animal #7 moved further south down IPM1 and also into a drainage channel between the 19/12/01 – 24/2/01. Movements north along IPM1 just prior to the month of December between the 19/11/01 – 19/12/01 were also evident. Animal #7 was not found after the 17/4/02.



Animal #8

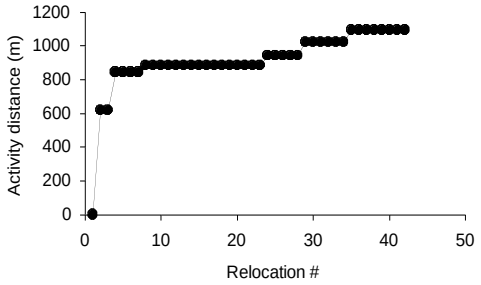


Figure 6.29: Left: Long-term movements of animal #8 (SVL = 500 mm, Sex = ♂) in IPM1, S2, swamp adjacent IPM1 and a Drainage Channel, outline indicates the position of a seasonal (wet season) swamp adjacent the IPM1. Areas used during all daily observations also indicated (grey). Above: Activity distance accumulated after each subsequent positional fix following release.

Table 6.29: Length, width and area of total activity areas and core activity areas (CAA).

Site	Total Length (m)	Approx width (m)	Area (m^2)	CAA length (m)	Width (m)	Area (m^2)
Channels + Drain + swamp	1039	100	103900	1039	100	103900

Long-term movements: Animal #8 used a length of the combined IPM1, S2, swamp and a length of Drainage Channel. It used one core activity area a length of the combined IPM1, S2, swamp and drainage channel. It was not found outside this core activity area. Fixes during mating season months showed animal #8 began moving north along IPM1 on the 14/1/01. After the 4/2/02 animal #8 moved to an unknown location for a period of 5 months. Animal #8 was not found after the 10/7/02.

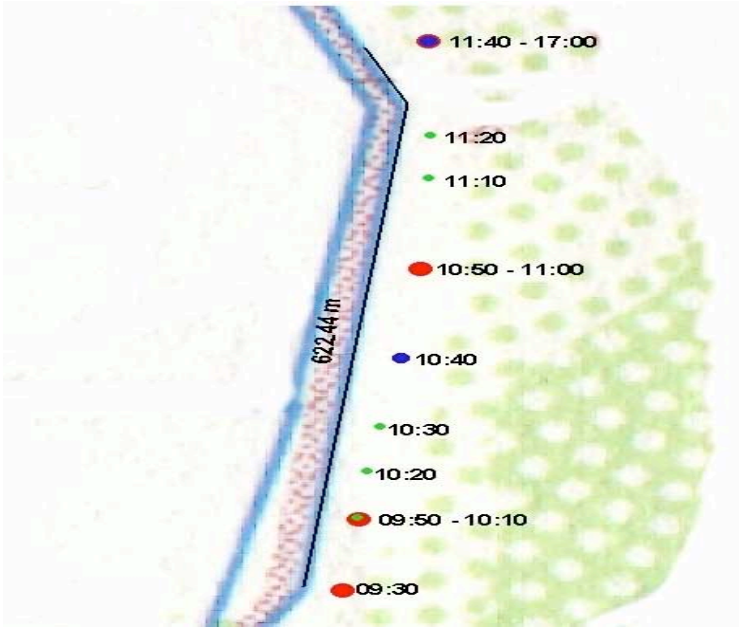


Figure 6.30: Daily movements of animal #8 in the IPM1 on the 19/10/01.

Table 6.30: Areas where different behaviours were undertaken and their duration.

Behaviour	Time (mins)	Location
Basking	180	Channel
Swimming	90	Channel
Foraging (walking)	40	Channel banks
Foraging (swimming)	10	Channel
Walking	10	Banks of channel

Daily movements: Included a section of IPM1of length 622 m and area 12440 m². The individual remained within channel throughout the day. Distance moved 635 m equating to a speed of 1.41 m min^{-1}. No burrow locations observed being used.

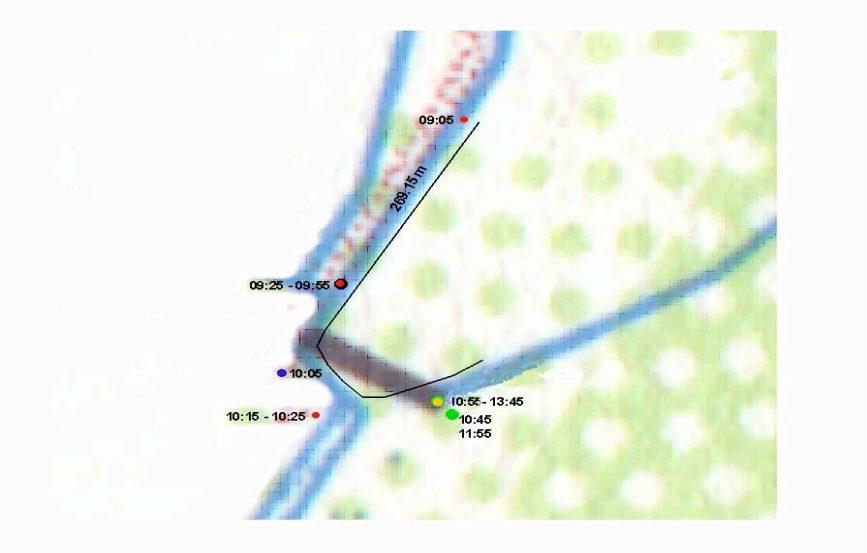
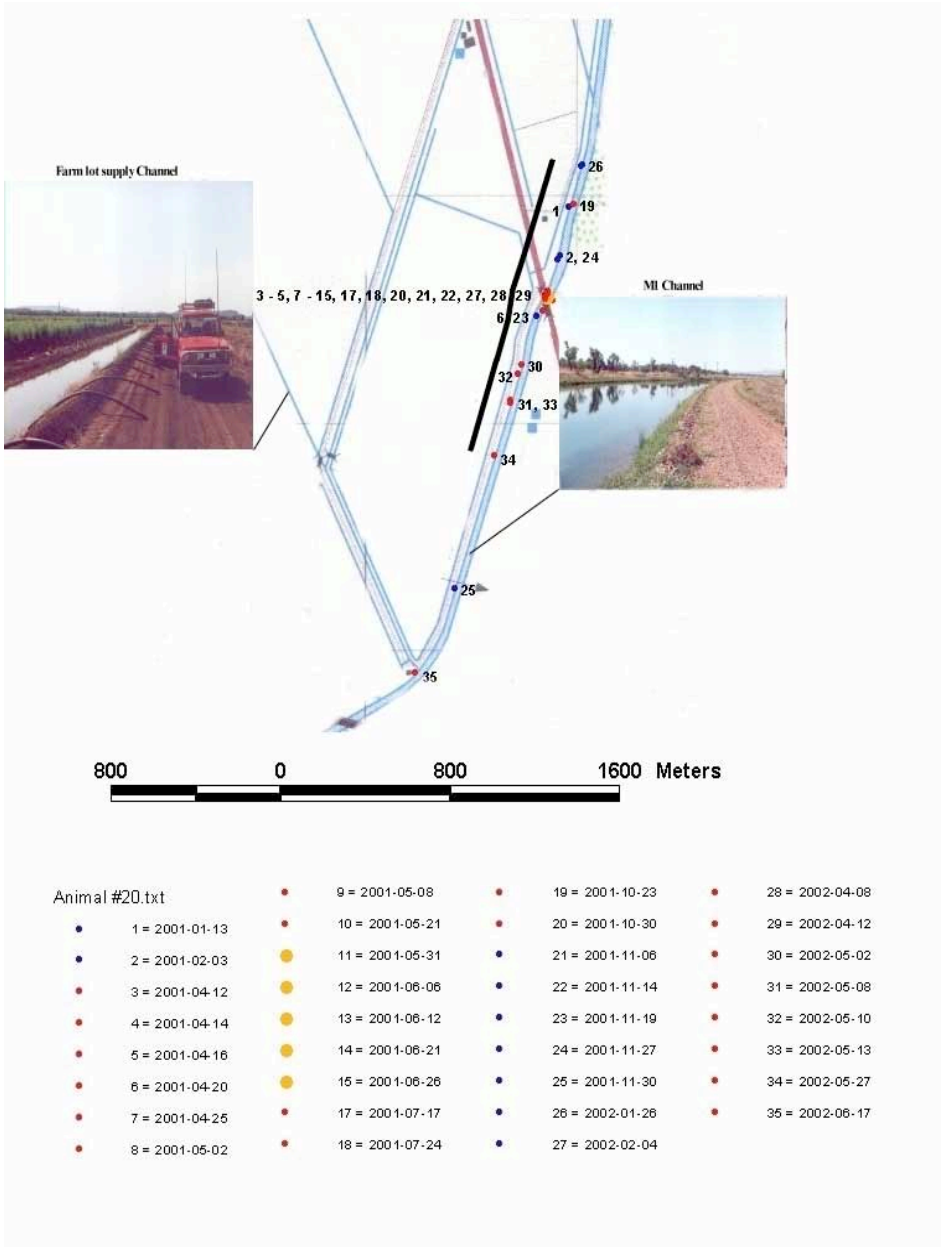


Figure 6.31: Daily movements of animal #8 in the IPM1 and drainage channel on the 10/12/01.

Table 6.31: Areas where different behaviours were undertaken and their duration.

Behaviour	Time (mins)	Location
Basking	70	Banks of channel
Swimming	10	Channel
Foraging (swimming)	20	Channel
Walking	10	Banks of channel

Daily movements: Included a section of IPM1 and a Drainage Channel with a length 269 m and area 5380 m². Distance moved 367 m equating to a speed of 2.04 m min^{-1}. The individual remained within both irrigation channels throughout the day until it retreated into a burrow at 10:55 hrs where it remained until the observation day was terminated at 13:45 hrs. One burrow in the bank of the drainage channel used upon retreat.



Animal #20

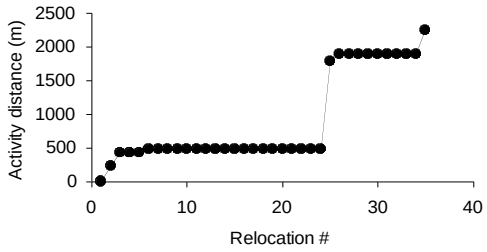
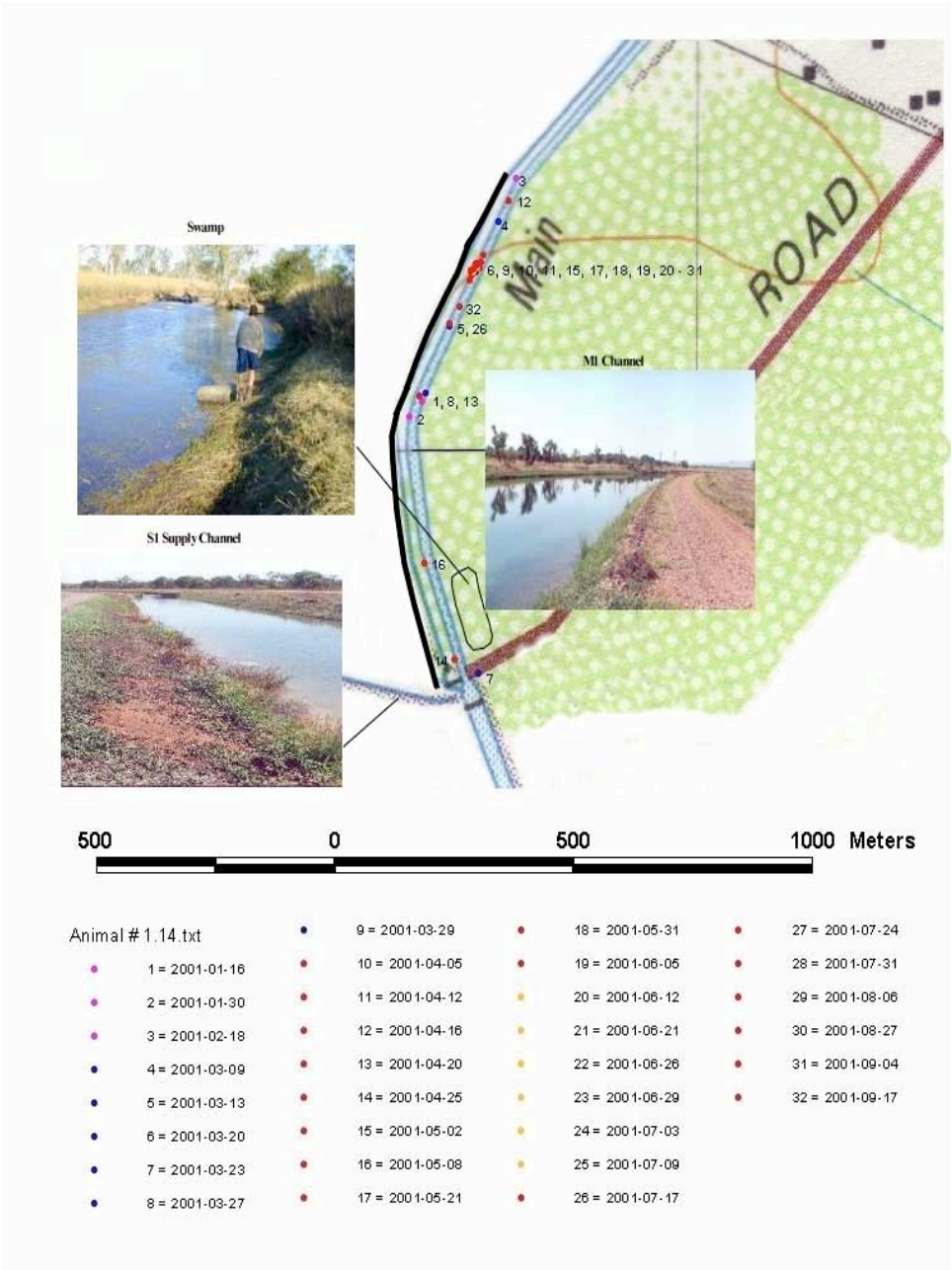


Figure 6.32: Left: Long-term movements of animal #20 (SVL = 420 mm, Sex = UC) in the IPM1. Above: Activity distance accumulated after each subsequent positional fix following release.

Table 6.32: Length, width and area of total activity areas and core activity areas (CAA).

Site	Total Length (m)	Width (m)	Area (m^2)	CAA length (m)	Width (m)	Area (m^2)
Channel	2248	20	44960	1380	20	27600

Long-term movements: Animal #20 used a length of IPM1. It used one core activity area a length of IPM1. It was only found outside this area on the 30/11/01 and the 17/6/02. Animal #20 burrowed and became inactive within its core activity area between the 31/5/01 – 26/6/01. A positional fix recorded on the 17/6/02 outside the core activity area of animal #20 suggests it was moving in search of a new activity area. In support of this animal # 20 was not found after the 17/6/02.



Animal #1.14

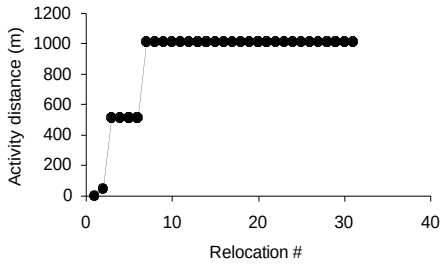
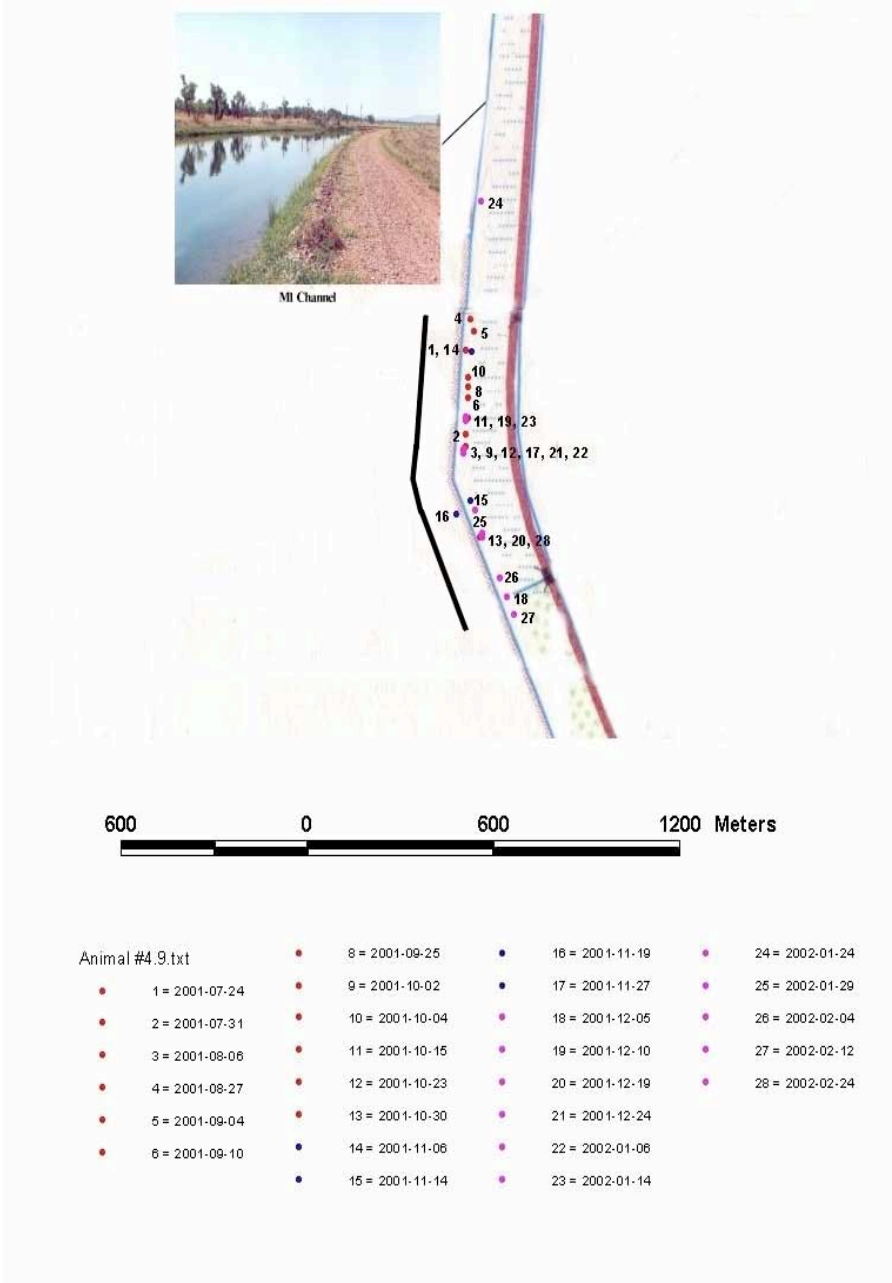


Figure 6.33: Left: Long-term movements of animal #1.14 (SVL = 390 mm, Sex = ♂) in the IPM1, outline indicates the position of a seasonal (wet season) swamp adjacent the IPM1. Above: Activity distance accumulated after each subsequent positional fix following release.

Table 6.33: Length, width and area of total activity areas and core activity areas (CAA).

Site	Total Length (m)	Width (m)	Area (m^2)	CAA length (m)	Width (m)	Area (m^2)
Channel	2248	20	44960	2248	20	44960

Long-term movements: Animal #1.14 used a length of IPM1. It used one core activity area a length of the IPM1. It was not found outside this area. Fixes during mating season months showed animal #1.14 moved north along IPM1 during February as indicated by a fix on the 18/2/01. Animal #1.14 was not found after the 17/9/01.



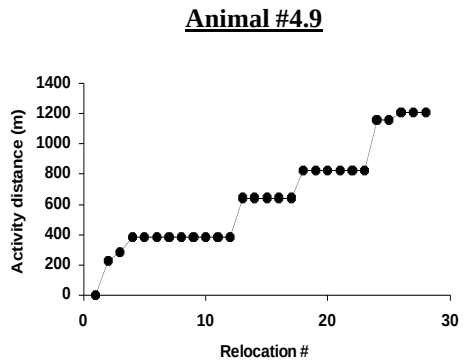
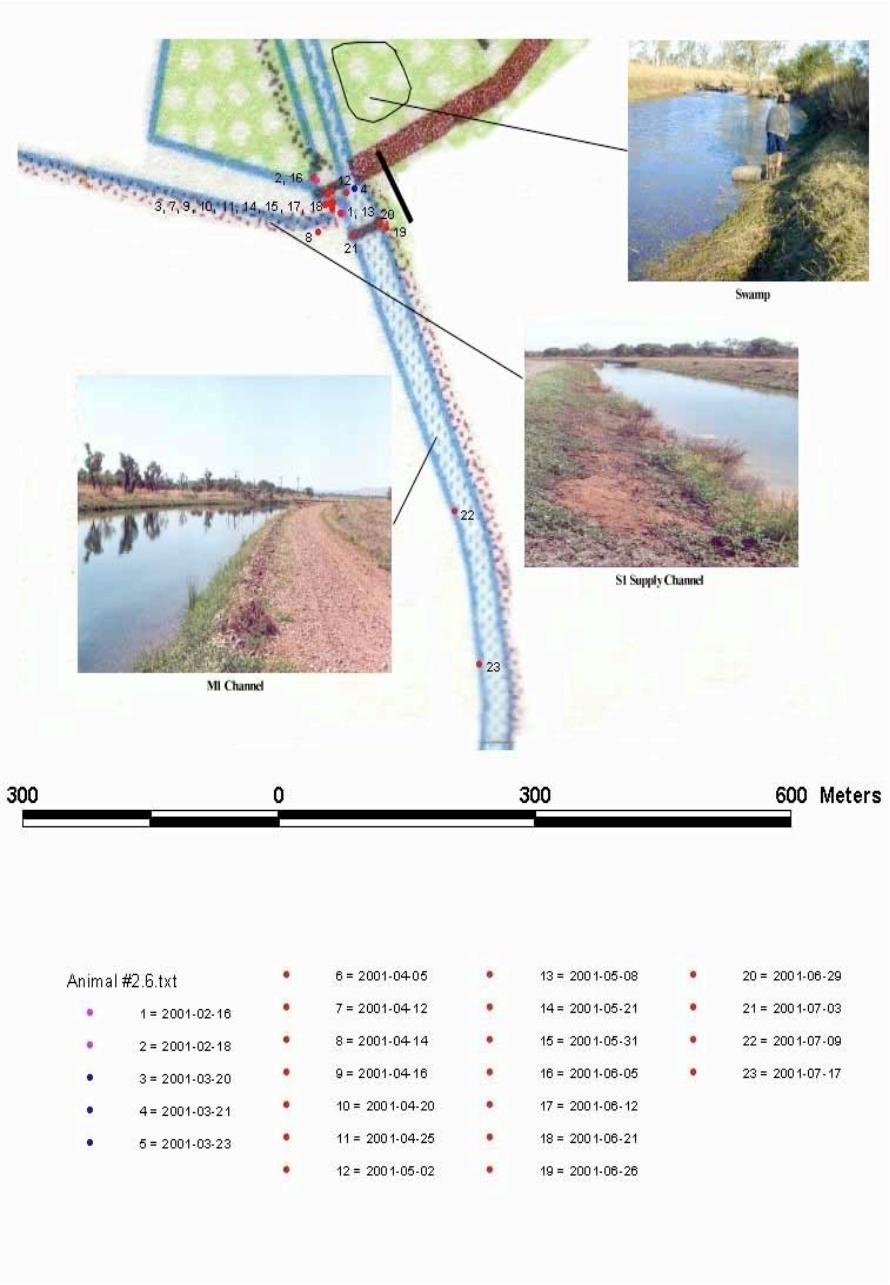


Figure 6.34: Left: Long-term movements of animal #4.9 (SVL = 460 mm, Sex = ♀) in the IPM1. Above: Activity distance accumulated after each subsequent positional fix following release.

Table 6.34: Length, width and area of total activity areas and core activity areas (CAA).

Site	Total Length (m)	Width (m)	Area (m^2)	CAA length (m)	Width (m)	Area (m^2)
Channel	1210	20	24200	893	20	17860

Long-term movements: Animal #4.9 used a length of IPM1. It used one core activity area a length of the IPM1. It was only found outside this area on the 24/1/02. Fixes during mating season months show animal #4.9 moved both south and north along IPM1 during the period 5/12/01 – 24/2/02. Animal #4.9 was not found after the 24/2/02.



Animal #2.6

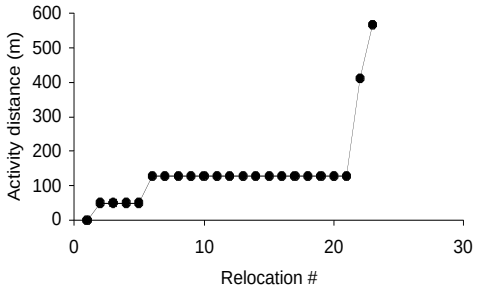
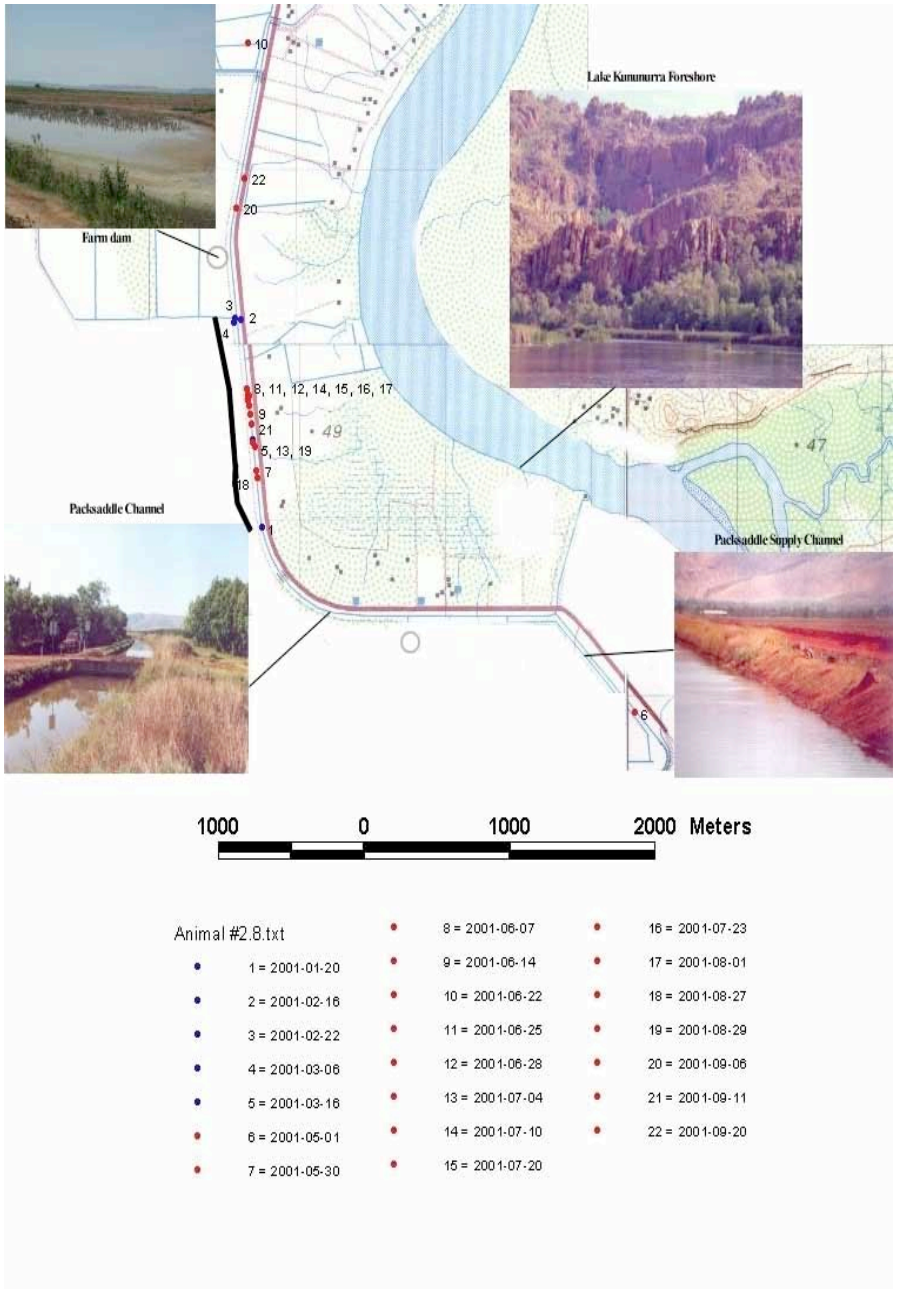


Figure 6.35: Left: Long-term movements of animal #2.6 (SVL = 510 mm, Sex = UC) in the IPM1. Above: Activity distance accumulated after each subsequent positional fix following release.

Table 6.35: Length, width and area of total activity areas and core activity areas (CAA).

Site	Total Length (m)	Width (m)	Area (m^2)	CAA length (m)	Width (m)	Area (m^2)
Channel	565	20	11300	85	20	1700

Long-term movements: Animal #2.6 used a length of IPM1. It used one core activity area a length of the IPM1. It was only found outside this area on the 5/4/01, 9/7/01 and 17/7/01. Positional fixes recorded on the 9/7/01 and 17/7/01 outside the core activity area of animal #2.6 suggests it was moving in search of a new activity areas. In support of this animal #2.6 was not found after the 17/7/01.



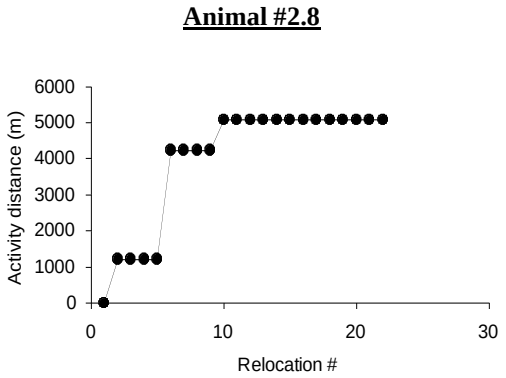
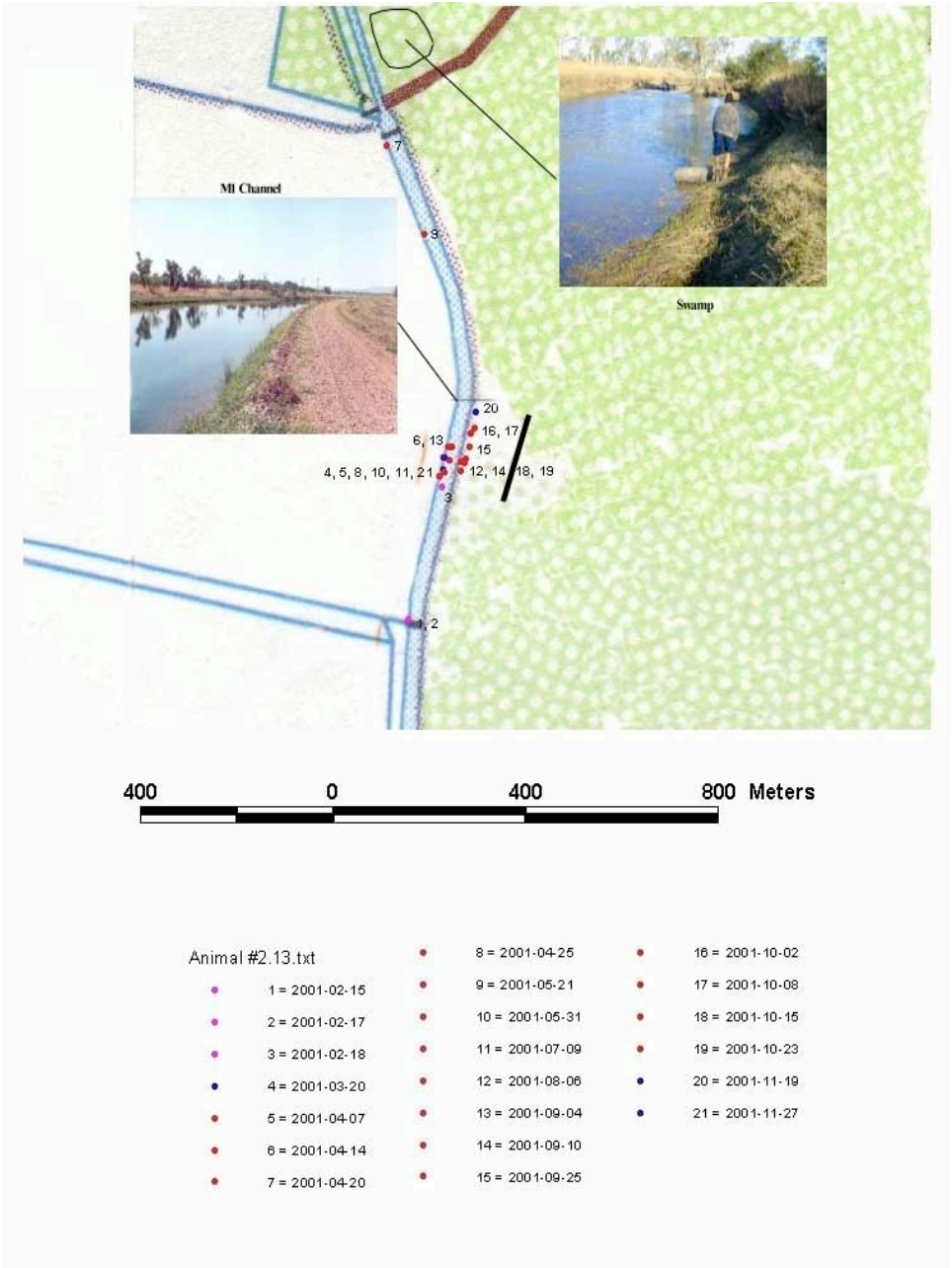


Figure 6.36: Left: Long-term movements of animal #2.8 (SVL = 390 mm, Sex = UC) in PSMIC, circles indicate the position of farm dams 1 and 2 adjacent the PSMIC. Above: Activity distance accumulated for each subsequent positional fix following release.

Table 6.36: Length, width and area of total activity areas and core activity areas (CAA).

Site	Total Length (m)	Width (m)	Area (m^2)	CAA length (m)	Width (m)	Area (m^2)
Channel	5070	10	50700	1240	10	12400

Long-term movements: Animal #2.8 used a length of the PSMIC. It used one core activity area a length of the PSMIC. It was only found outside this area upon capture and release on the 20/1/01 and subsequently on the 1/5/01, 22/6/01, 6/9/01 and 20/9/01. Animal #2.8 was not found after the 20/9/01.



Animal #2.13

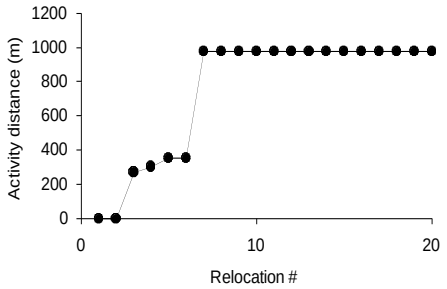
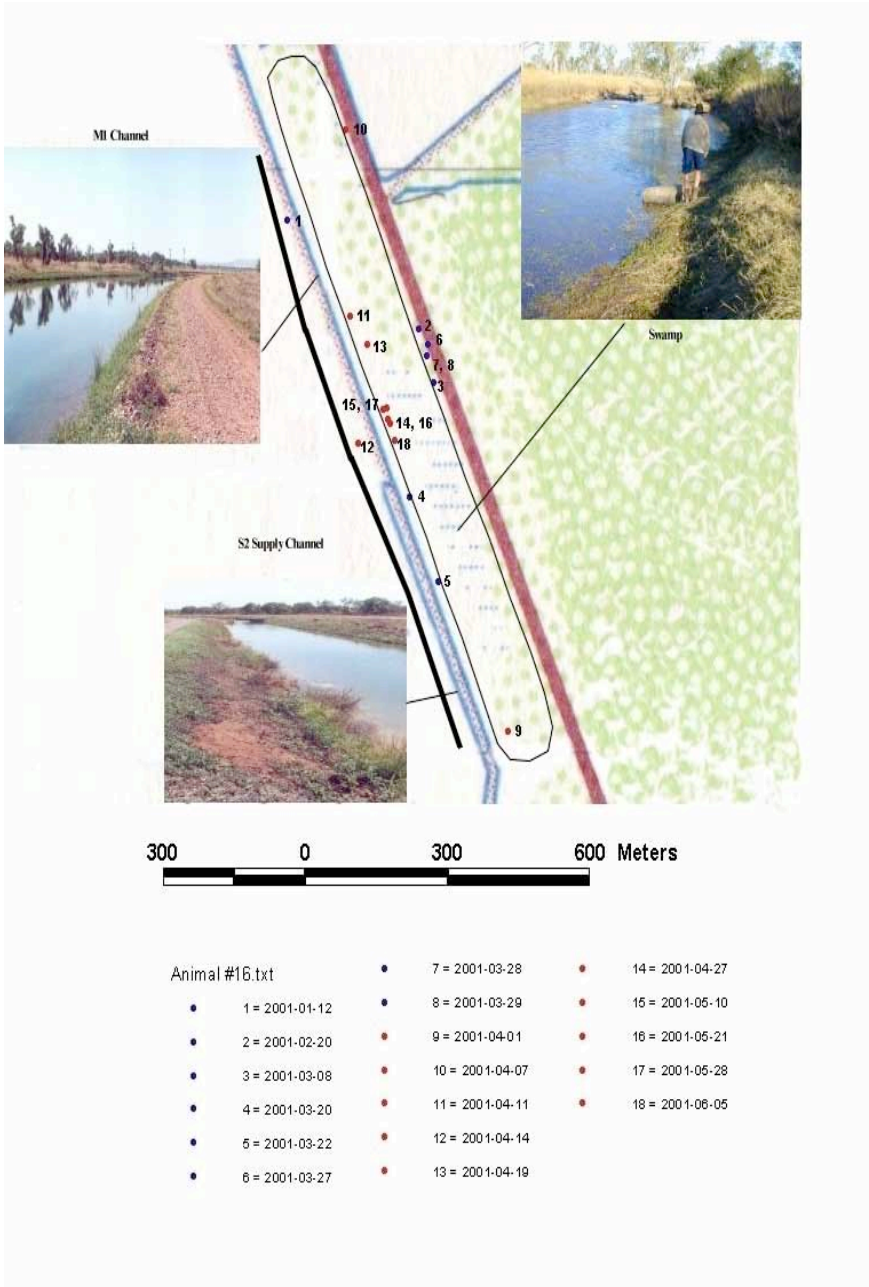


Figure 6.37: Left: Long-term movements of animal #2.13 (SVL = 500 mm, Sex = ♀) in the IPM1. Above: Activity distance accumulated for each subsequent positional fix following release.

Table 6.37: Length, width and area of total activity areas and core activity areas (CAA).

Site	Total Length (m)	Width (m)	Area (m^2)	CAA length (m)	Width (m)	Area (m^2)
Channel	976	20	19520	166	20	3320

Long-term movements: Animal #2.13 used a length of the IPM1. It used one core activity area a length of the IPM1. It was only found outside this area upon capture and release on the 15/2/01 and subsequently on the 17/2/01, 20/4/01 and 21/5/01. Fixes during mating season months show animal #2.13 moved south along the IPM1 during the period 15/2/01 – 18/2/01. Animal #2.13 was not found after the 27/11/01.



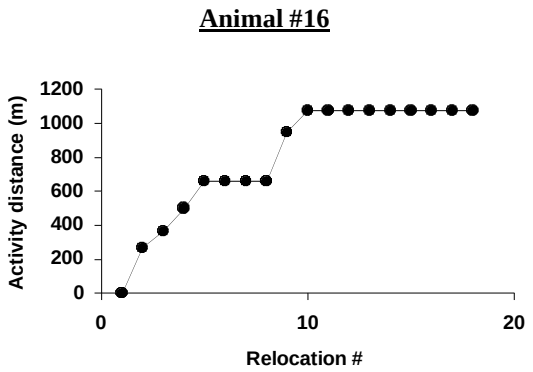
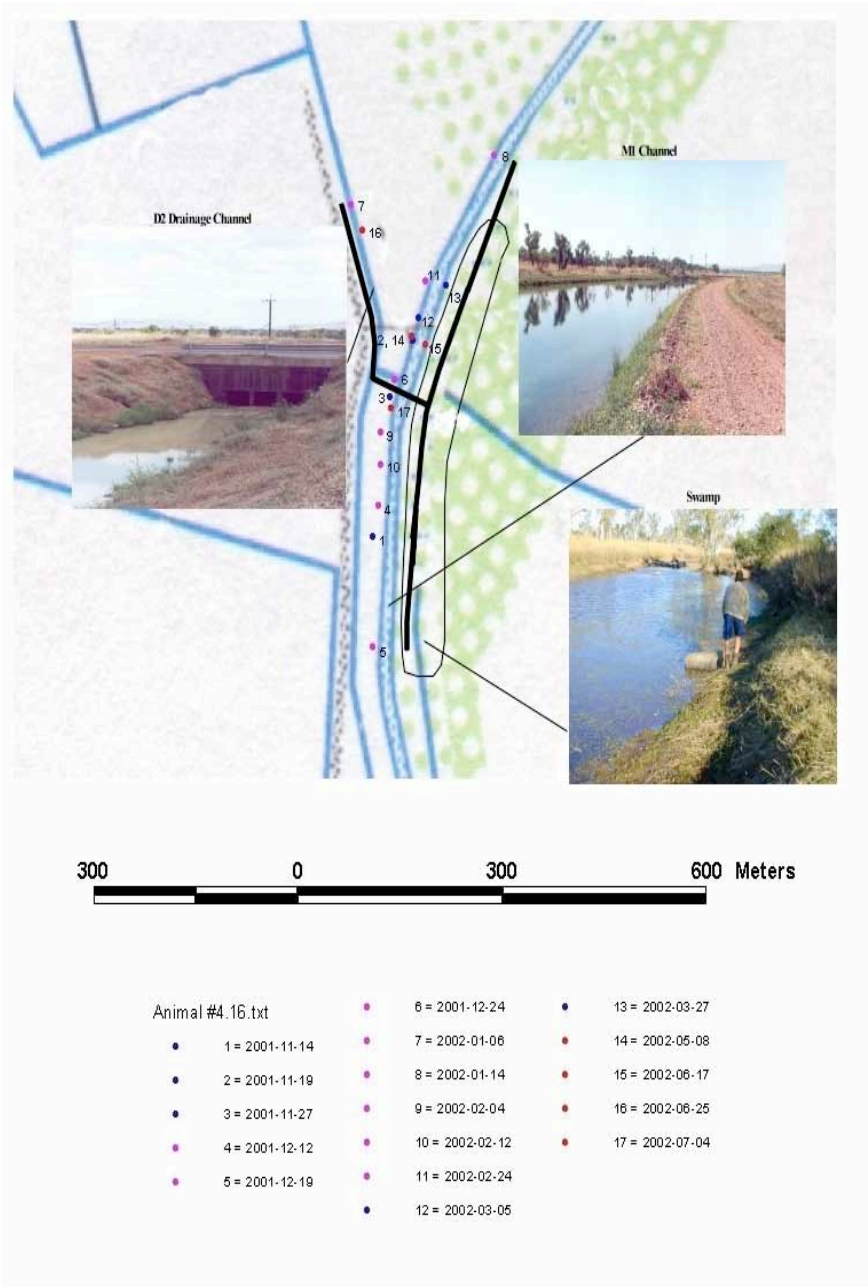


Figure 6.38: Left: Long-term movements of animal #16 (SVL = 460 mm, Sex = UC) in the IPM1, S2 and adjacent swamp. Above: Activity distance accumulated for each subsequent positional fix following release.

Table 6.38: Length, width and area of total activity areas and core activity areas (CAA).

Site	Total Length (m)	Width (m)	Area (m^2)	Length of CAA's (m)	Width (m)	Area (m^2)
Channel + S2 + swamp	1075	100	107500	1075	100	107500

Long-term movements: Animal #16 used a length of the combined IPM1, S2 and swamp. It used one core activity area a length of the combined IPM1, S2 and swamp. It was not found outside this area. Animal #16 was not found after the 5/6/01.



Animal #4.16

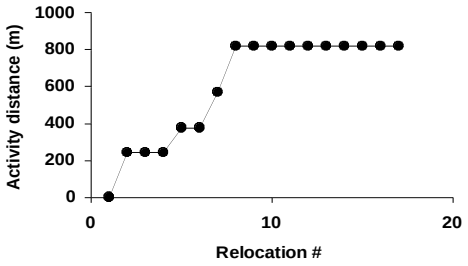
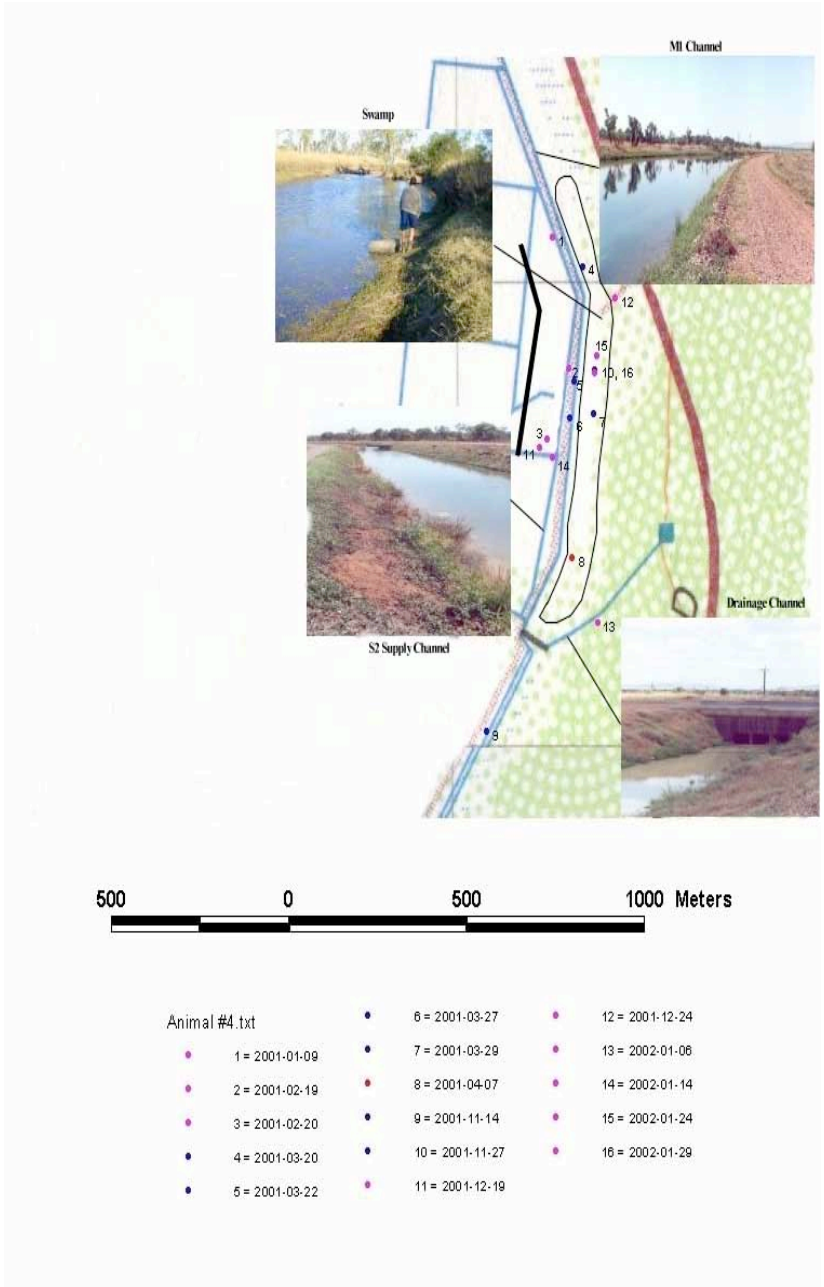


Figure 6.39: Left: Long-term movements of animal #4.16 (SVL = 370 mm, Sex = ♂) in the IPM1 and D1, outline indicates the position of a seasonal (wet season) swamp adjacent IPM1. Above: Activity distance accumulated for each subsequent positional fix following release.

Table 6.39: Length, width and area of total activity areas and core activity areas (CAA).

Site	Total Length (m)	Width (m)	Area (m^2)	Length of CAA's (m)	Width (m)	Area (m^2)
Channels	820	20	16400	312	820	16400

Long-term movements: Animal #4.16 used a length of both the IPM1 and D1. It used one core activity area a length of the IPM1. It was not found outside this area. Fixes during mating season months showed animal #4.16 moved south along IPM1 as indicated by a fix on the 19/12/01, north along D1 as indicated by a fix on the 6/1/02 and north along IPM1 as indicated by a fix on the 14/1/02. Animal #4.16 was not found after the 4/7/02.



Animal #4

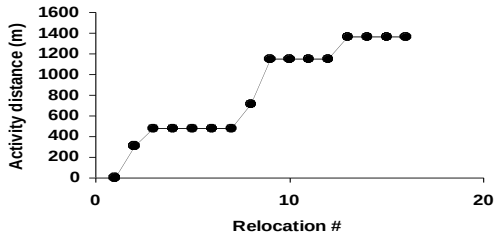
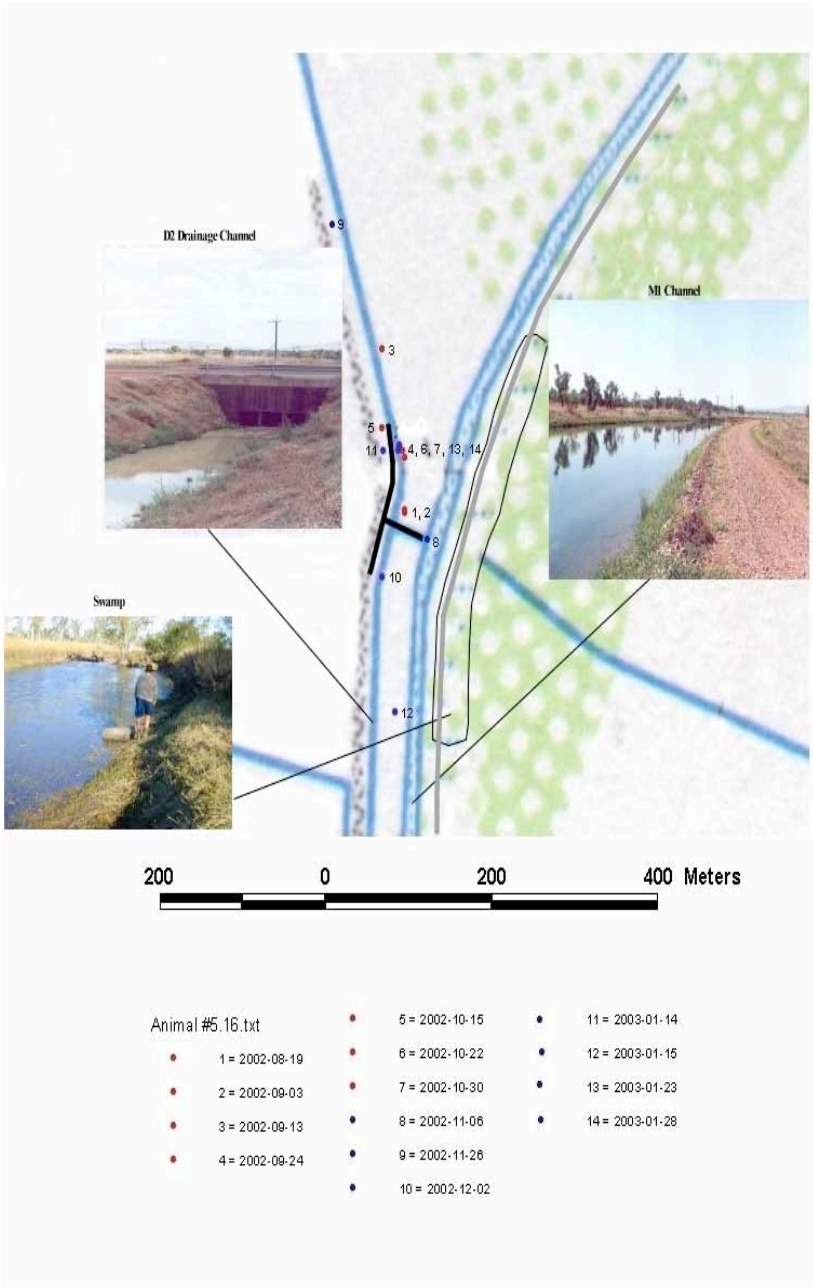


Figure 6.40: Left: Long-term movements of animal #4 (SVL = 450 mm, Sex = UC) in the IPM1, S2 and adjacent swamp. Above: Activity distance accumulated for each subsequent positional fix following release.

Table 6.40: Length, width and area of total activity areas and core activity areas (CAA).

Site	Total Length (m)	Width (m)	Area (m^2)	Length of CAA's (m)	Width (m)	Area (m^2)
Channels + swamp	1365	100	136500	473	100	47300

Long-term movements: Animal #4 used a length of the combined IPM1, S2 and swamp and a drainage channel. It used one core activity area a length of the combined IPM1, S2 and a swamp. It was only found outside this area on the 7/4/01, 14/11/01 and the 5/1/02. Animal #4 was not found after the 29/1/02.



Animal #5.16

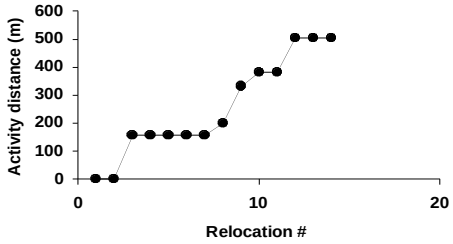


Figure 6.41: Left: Long-term movements of animal #5.16 (SVL = 400 mm, Sex = UC) in the IPM1 and D1, outline indicate position of a seasonal (wet season) swamp adjacent the IPM1. Areas used during all daily observations also indicated (grey). Above: Activity distance accumulated for each subsequent positional fix following release.

Table 6.41: Length, width and area of total activity areas and core activity areas (CAA).

Site	Total Length (m)	Width (m)	Area (m^2)	Length of CAA's (m)	Width (m)	Area (m^2)
Channels	1510	20	30200	202	5	1010

Long-term movements: Animal #5.16 used a length of the IPM1 and D1. Interestingly, animal #5.16 observed on the 16/1/03 used a daily activity area substantially larger that its total activity area suggesting it may have been searching for a new activity area on this day. These daily movements were included in the total activity area of animal #5.16. It used one core activity area a length of D1. It was only found outside this area on the 13/9/01, 26/11/02 and 15/1/03. Animal #5.16 was not found after the 28/1/03.

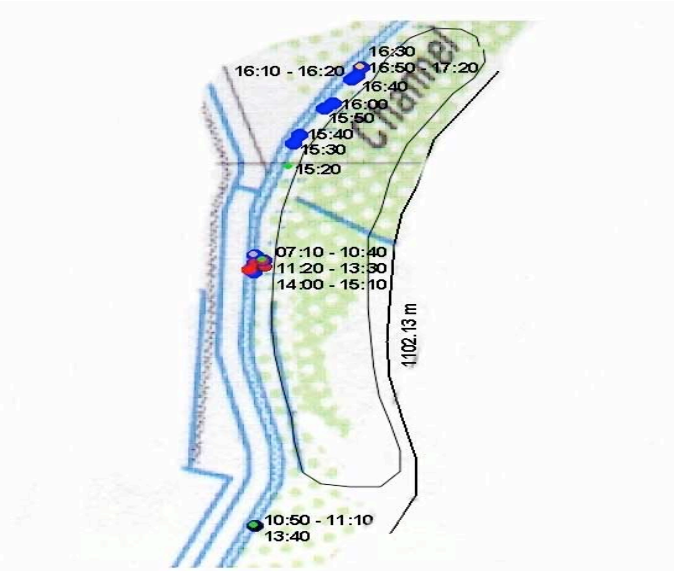


Figure 6.42: Daily movements of animal #5.16 in the IPM1 on the 16/1/03. Outline indicates the position of a seasonal (wet season) swamp adjacent the IPM1.

Table 6.42: Areas where different behaviours were undertaken and their duration.

Behaviour	Time (mins)	Location
Basking	130	Banks of swamp/ channel
Swimming	250	In swamp/ channel
Foraging (walking)	10	Banks of swamp/channel/access road
Foraging (swimming)	180	Swamp/channel
Walking	30	Banks of channel

Daily movements: Included a section of IPM1 of length 1102 m and area 22040 m². The individual remained in the IPM1 throughout the day. Distance moved 2871 m equating to a speed of movement of 4.79 m min^{-1}. Two separate burrows in the bank of IPM1 used prior to emergence and upon retreat.

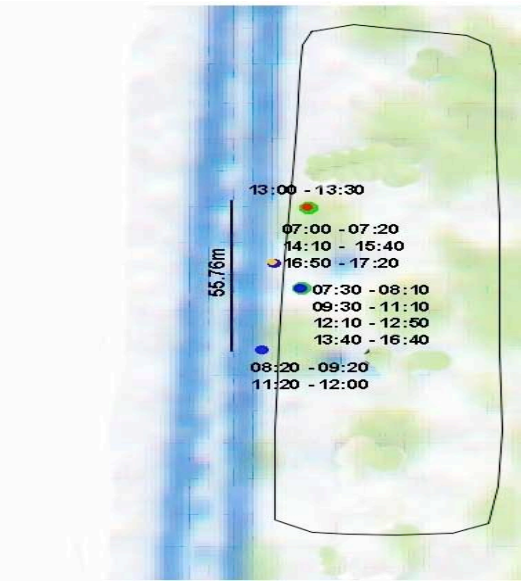
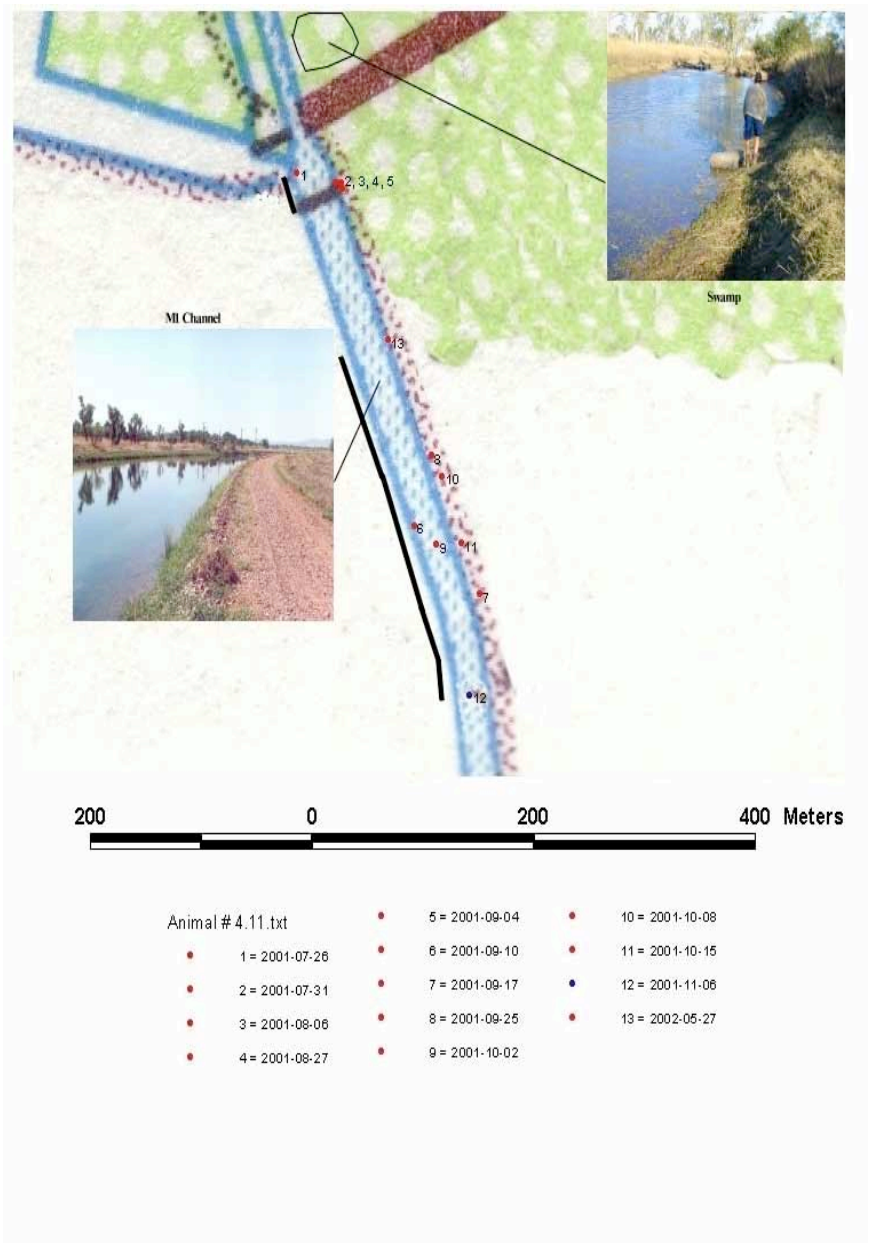


Figure 6.43: Daily movements of animal #5.16 in a seasonal (wet season) swamp adjacent the IPM1 on the 20/1/03. Outline indicates position of swamp.

Table 6.43: Areas where different behaviours were undertaken and their duration.

Behaviour	Time (mins)	Location
Basking	30	Banks of swamp
Swimming	480	In swamp
Walking	70	Banks of swamp

Daily movements: Included a section of a swamp with length 55 m and area 2750 m². Individual remained within the swamp area throughout the day until it retreated into a burrow at 16:50 hrs where it remained until the observation day was terminated at 17:20 hrs. Distance moved 181 m equating to a speed of 0.31 m min^{-1}. One burrow in the bank of the swamp used both prior to emergence and on retreat.



Animal #4.11

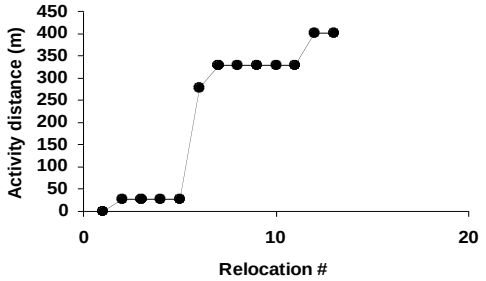
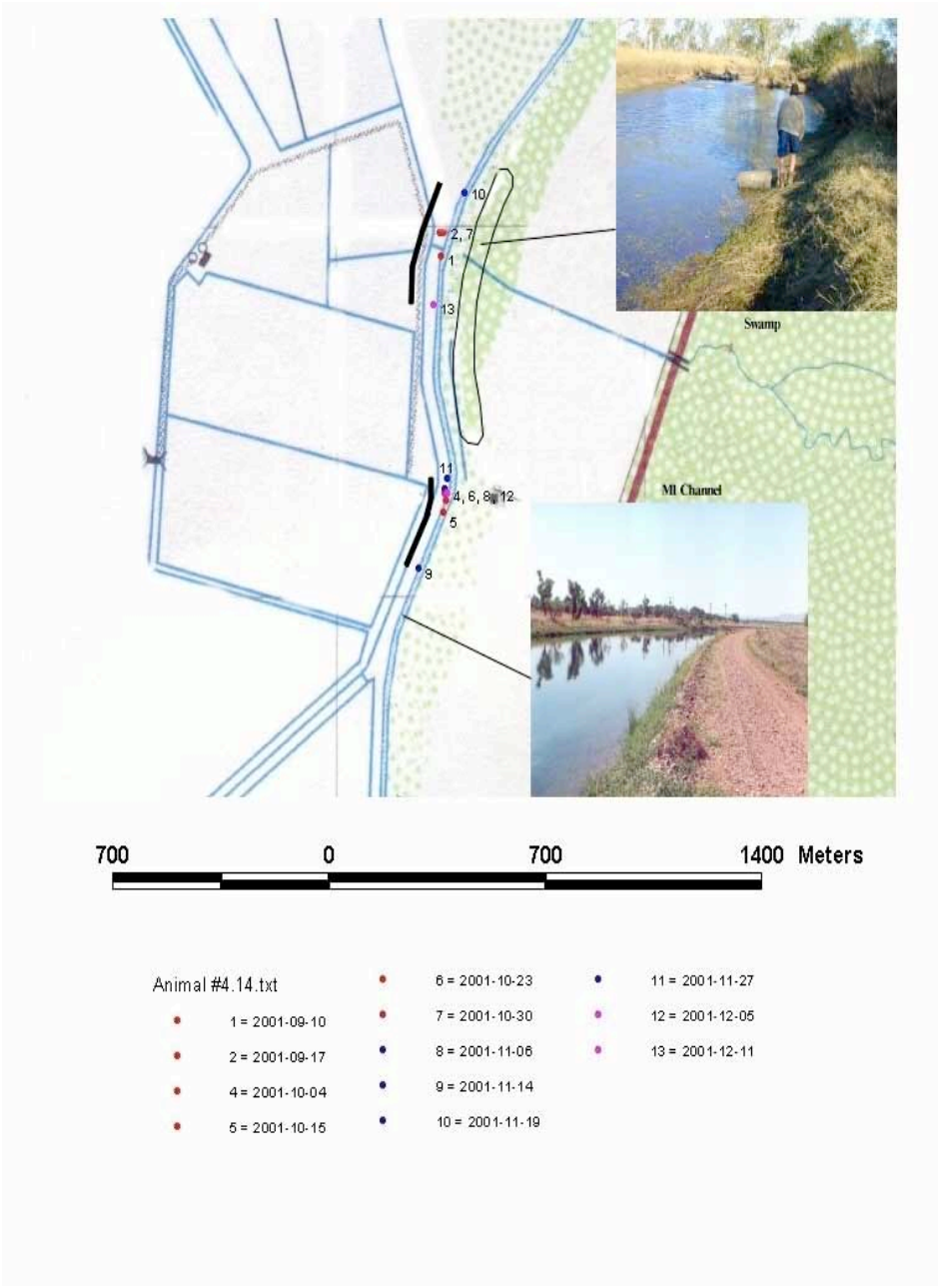


Figure 6.44: Left: Long-term movements of animal #4.11(SVL = 550 mm, Sex = UC) in the IPM1, Outline indicates position of a seasonal (wet season) swamp adjacent the IPM1. Above: Activity distance accumulated for each subsequent positional fix following release.

Table 6.44: Length, width and area of total activity areas and core activity areas (CAA)

Site	Total Length (m)	Width (m)	Area (m^2)	Length of CAA's (m)	Width (m)	Area (m^2)
Channel	402	20	8040	270	20	5400
Channel				30	20	600

Long-term movements: Animal #4.11 used a length of the IPM1. It used two core activity areas both a length of the IPM1. It was not found outside these areas. Animal #4.11 was not found after the 27/5/02.



Animal #4.14

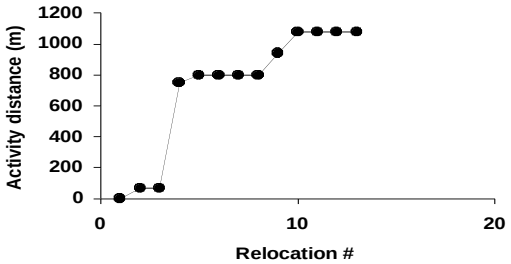
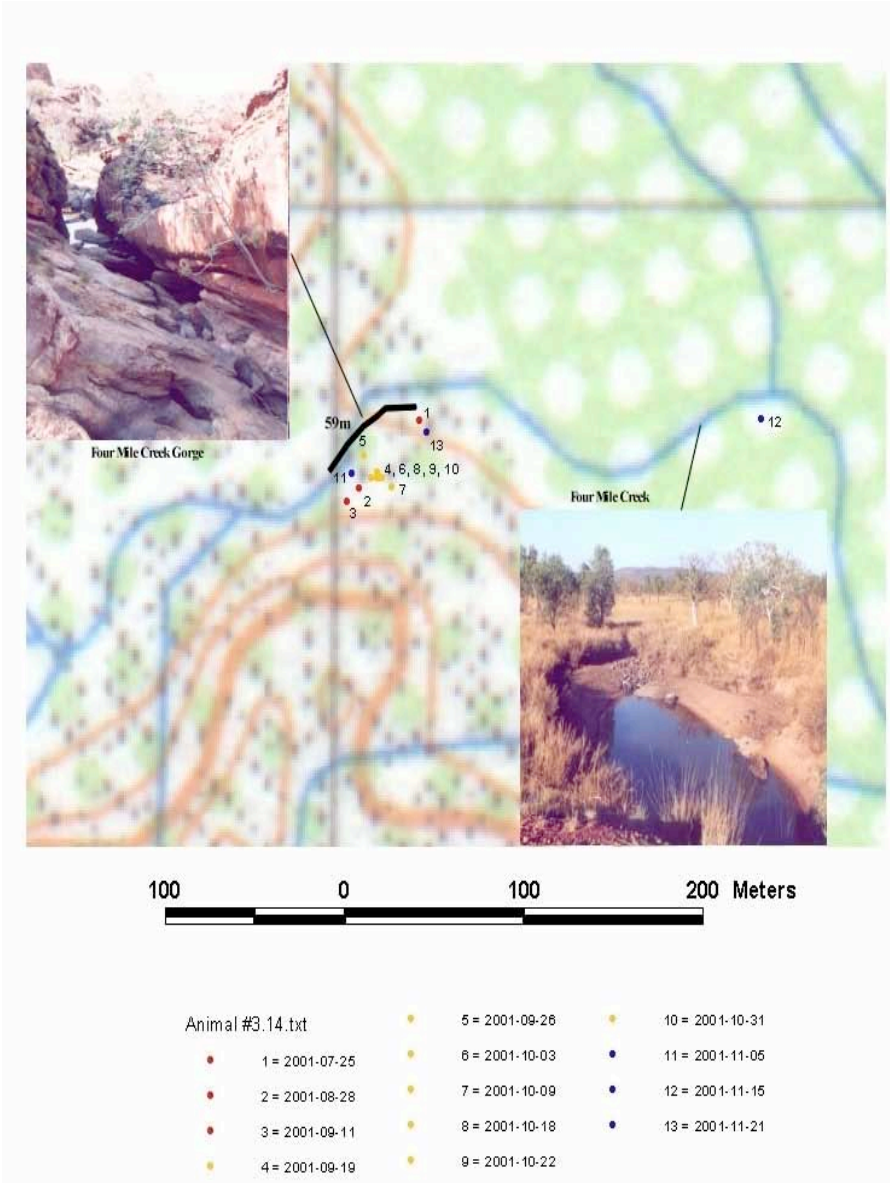


Figure 6.45: Left: Long-term movements of animal #4.14 (SVL = 450 mm, Sex = ♂) in the IPM1, outline indicates the position of a seasonal (wet season) swamp adjacent the IPM1. Above: Activity distance accumulated for each subsequent positional fix following release.

Table 6.45: Length, width and area of total activity areas and core activity areas (CAA).

Site	Total Length (m)	Width (m)	Area (m^2)	Length of CAA's (m)	Width (m)	Area (m^2)
Channel	1076	20	21520	335	20	6700
				261	20	5220

Long-term movements: Animal #4.14 used a length of the IPM1. It used two core activity areas both a length of the IPM1. It was not found outside these areas. Fixes during mating season months showed animal #4.14 moved north along IPM1 as indicated by a fix on the 11/12/01 before moving to an unknown location. Animal #4.14 was not found after the 11/12/01.



Animal #3.14

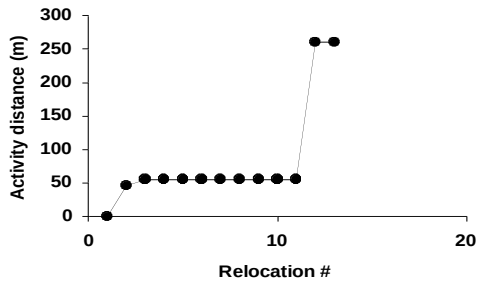
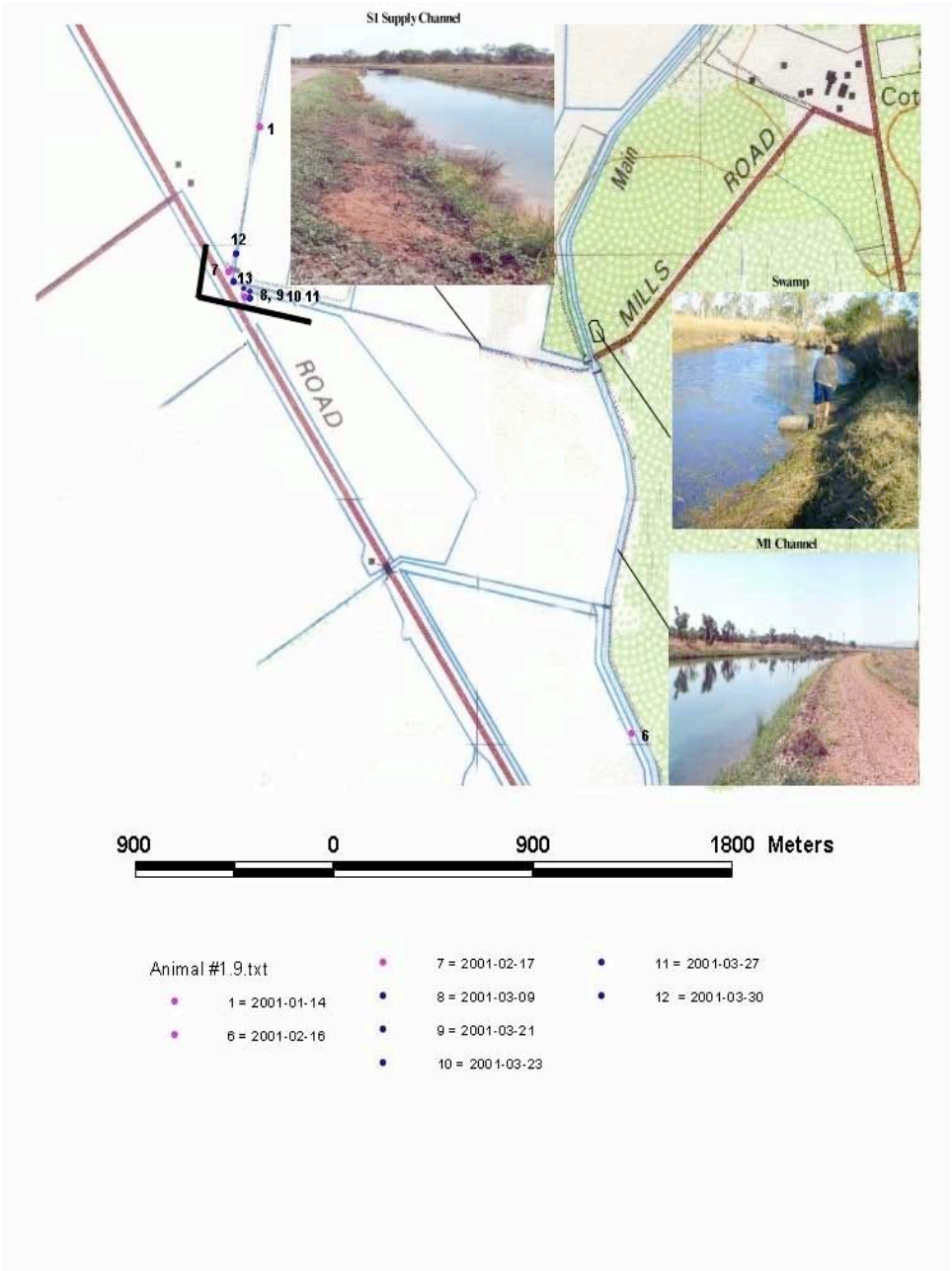


Figure 6.46: Left: Long-term movements of animal #3.14 (SVL = 400 mm, Sex = UC) in the Four Mile Creek (FMC). Above: Activity distance accumulated for each subsequent positional fix following release.

Table 6.46: Length, width and area of total activity areas and core activity areas (CAA).

Site	Total Length (m)	Width (m)	Area (m^2)	Length of CAA's (m)	Width (m)	Area (m^2)
Watercourse	260	5	1300	59	5	295

Long-term movements: Animal #3.14 used a length of the FMC including a gorge. It used one core activity area a length of the FMC Gorge. It was only found outside this area on the 15/11/01. Animal #3.14 burrowed and became inactive in its core activity area between the 19/9/01 – 31/10/01. Animal #3.14 was not found after the 21/11/02.



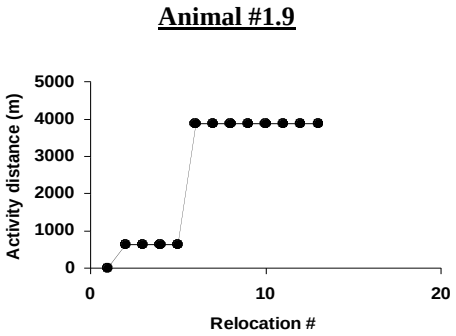
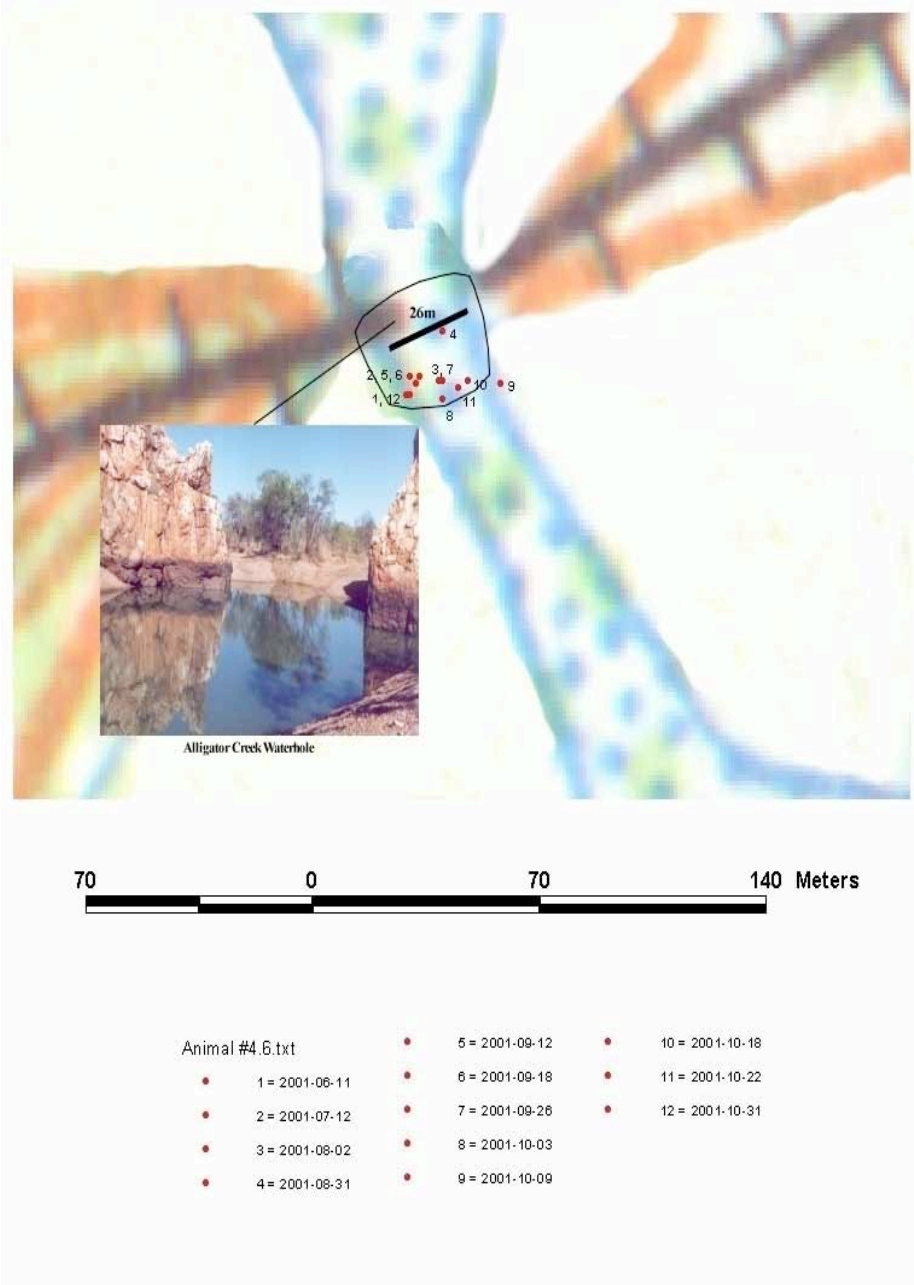


Figure 6.47: Left: Long-term movements of animal #1.9 (SVL = 385 mm, Sex = ♂) in the IPM1 and S1. Above: Activity distance accumulated for each subsequent positional fix following release.

Table 6.47: Length, width and area of total activity areas and core activity areas (CAA).

Site	Total Length (m)	Width (m)	Area (m^2)	Length of CAA's (m)	Width (m)	Area (m^2)
Channel	3876	20	77520	290	10	2900

Long-term movements: Animal #1.9 used a length of the IPM1 and S1. It used one core activity area a length of the S1. It was only found outside this area upon capture and release on the 14/1/01 and subsequently on the 16/2/01. Fixes during mating season months showed animal #1.9 moved into IPM1 and south as indicated by a fix on the 16/2/01. Animal #1.9 was not found after the 30/3/01.



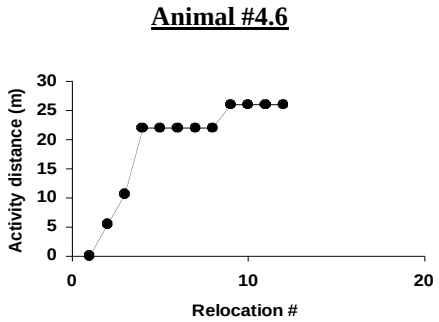
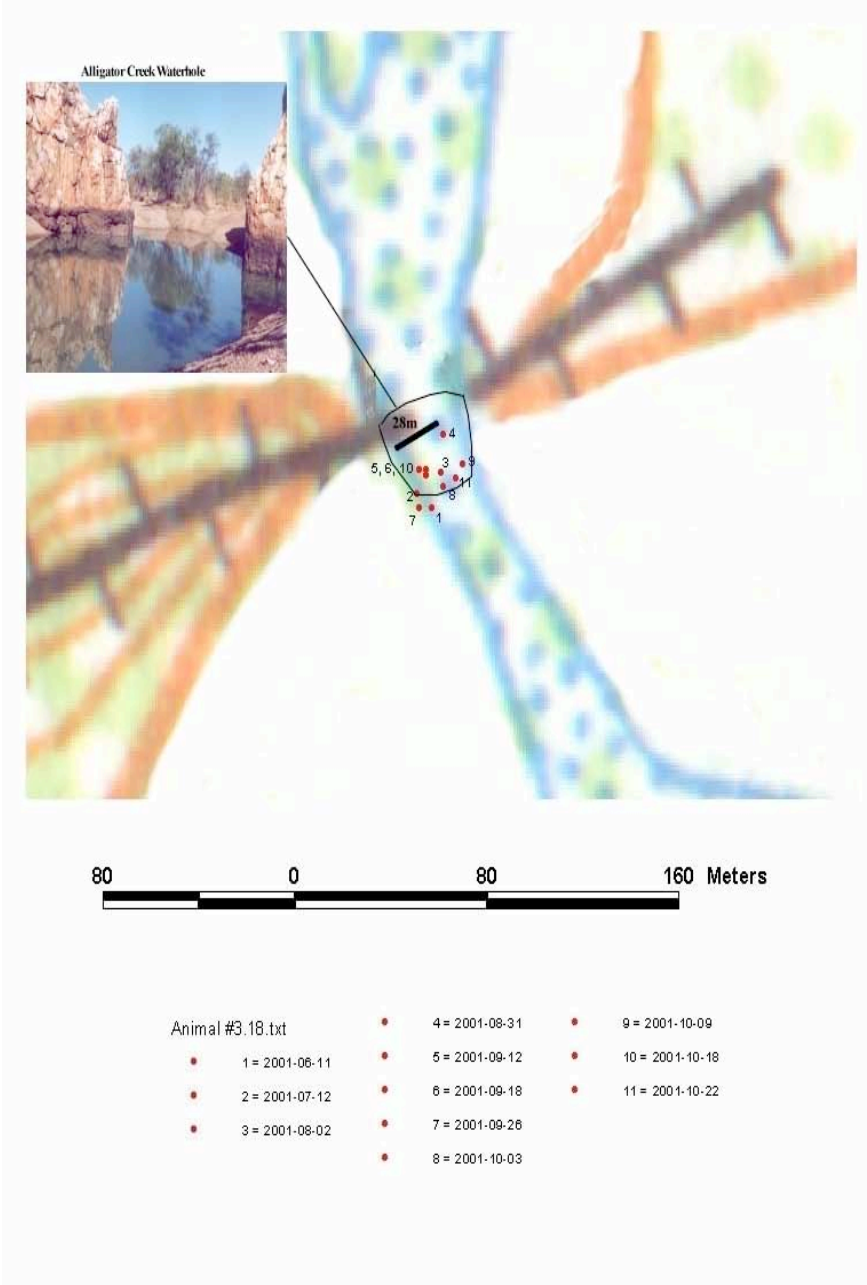


Figure 6.48: Left: Long-term movements of animal #4.6 (SVL = 440 mm, Sex = UC) in the Alligator Creek Waterhole (ACW), outline indicates the position of a perennial waterhole. Above: Activity distance accumulated for each subsequent positional fix following release.

Table 6.48: Length, width and area of total activity areas and core activity areas (CAA).

Site	Total Diameter (m)	Width (m)	Area (m^2)	Diameter of CAA's (m)	Width (m)	Area (m^2)
Waterhole	26		530	26		530

Long-term movements: Animal #4.6 used the ACW. It used one core activity area, the ACW. Animal #4.6 was not found after the 31/10/01.



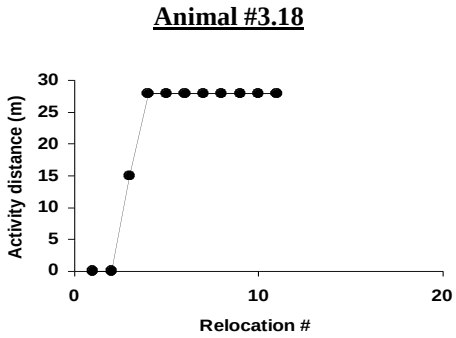
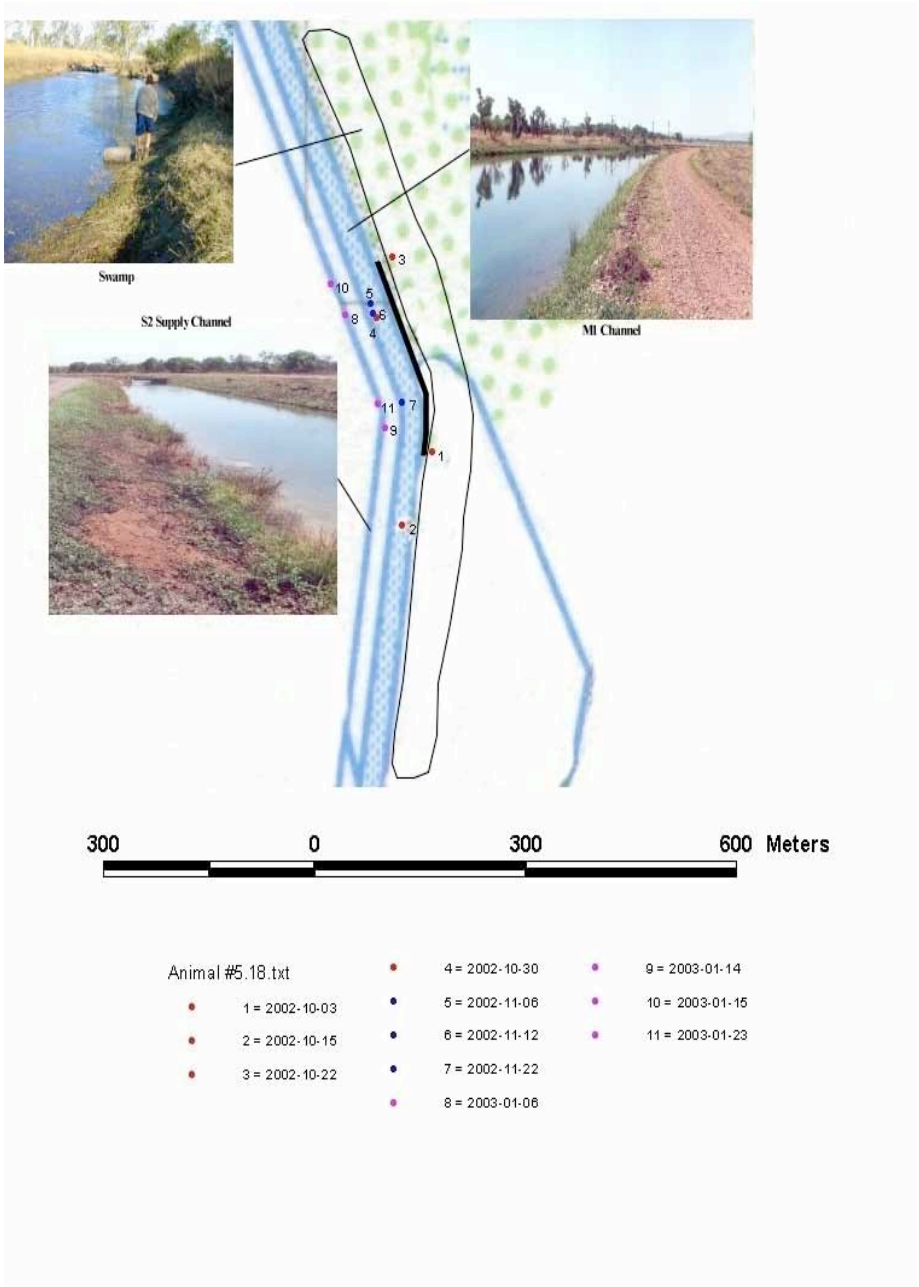


Figure 6.49: Left: Long-term movements of animal #3.18 (SVL = 430 mm, Sex = UC) in the ACW, Outline indicates the position of a perennial waterhole. Above: Activity distance accumulated for each subsequent positional fix following release.

Table 6.49: Length, width area of total activity areas and core activity areas (CAA).

Site	Total diameter (m)	Width (m)	Area (m^2)	Diameter of CAA's (m)	Width (m)	Area (m^2)
Waterhole	28		615	28		615

Long-term movements: Animal #3.18 used the ACW. It used one core activity area, the ACW. Animal #3.18 was not found after the 22/10/01.



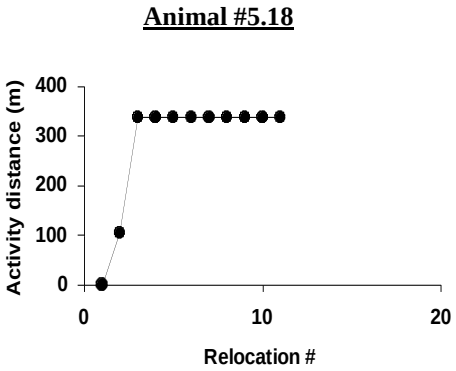
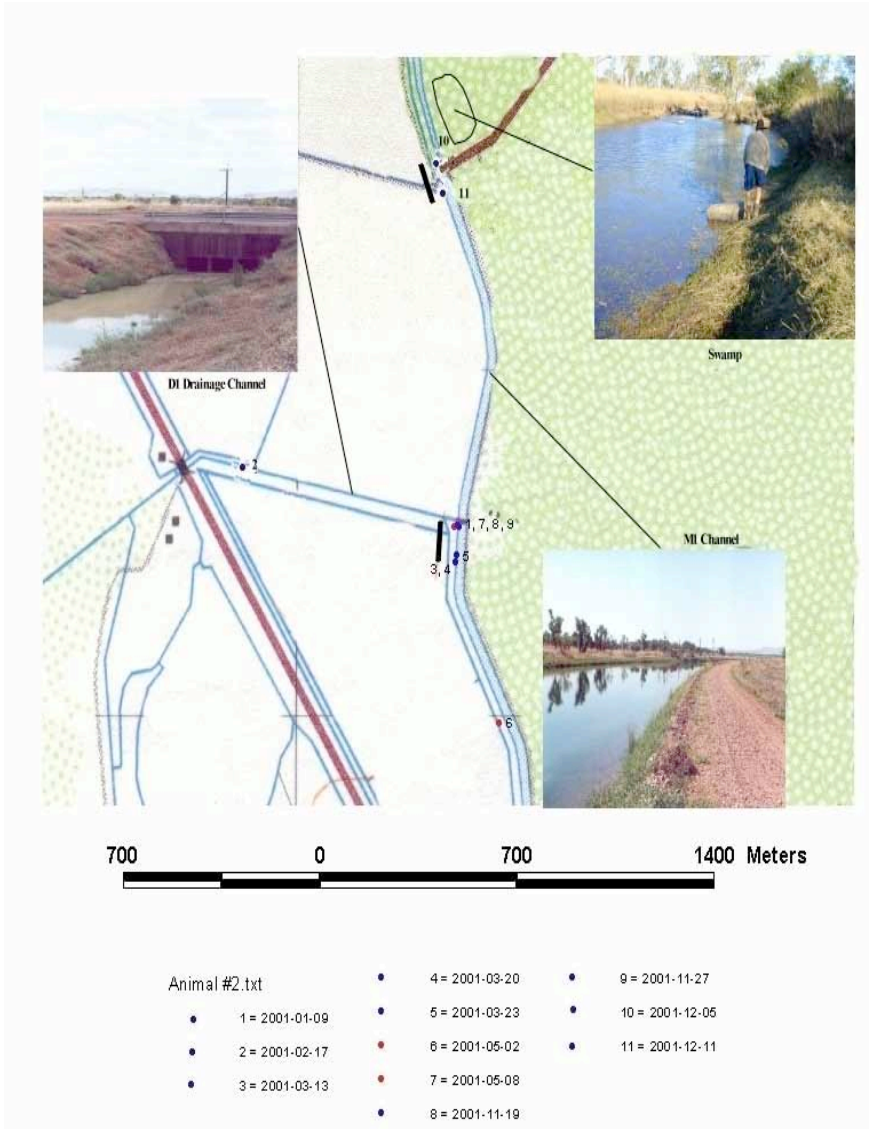


Figure 6.50: Long-term movements of animal #5.18 (SVL = 460 mm, Sex = ♂) in the IPM1, S2 and adjacent swamp, outline indicates the position of a seasonal (wet season) swamp adjacent the IPM1. Above: Activity distance accumulated for each subsequent positional fix following release.

Table 6.50: Length, width and area of total activity areas and core activity areas (CAA).

Site	Total Length (m)	Width (m)	Area (m^2)	Length of CAA's (m)	Width (m)	Area (m^2)
Channel s + swamp	337	100	33700	235	100	23500

Long-term movements: Animal #5.18 used a length of the combined IPM1, S2 and adjacent swamp. It used one core activity area a section of the combined IPM1, S2 and swamp. It was only found outside this area soon after capture release on the 15/10/02. Fixes during mating season months showed animal #5.18 moved from IPM1 and a swamp on the eastern side IPM1 to S2 as indicated by fixes on the 6/1/03, 14/1/03, 15/1/03 and 23/1/03. Animal #5.18 was not found after the 23/1/03.



Animal #2

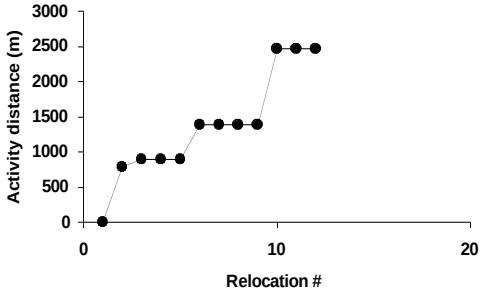
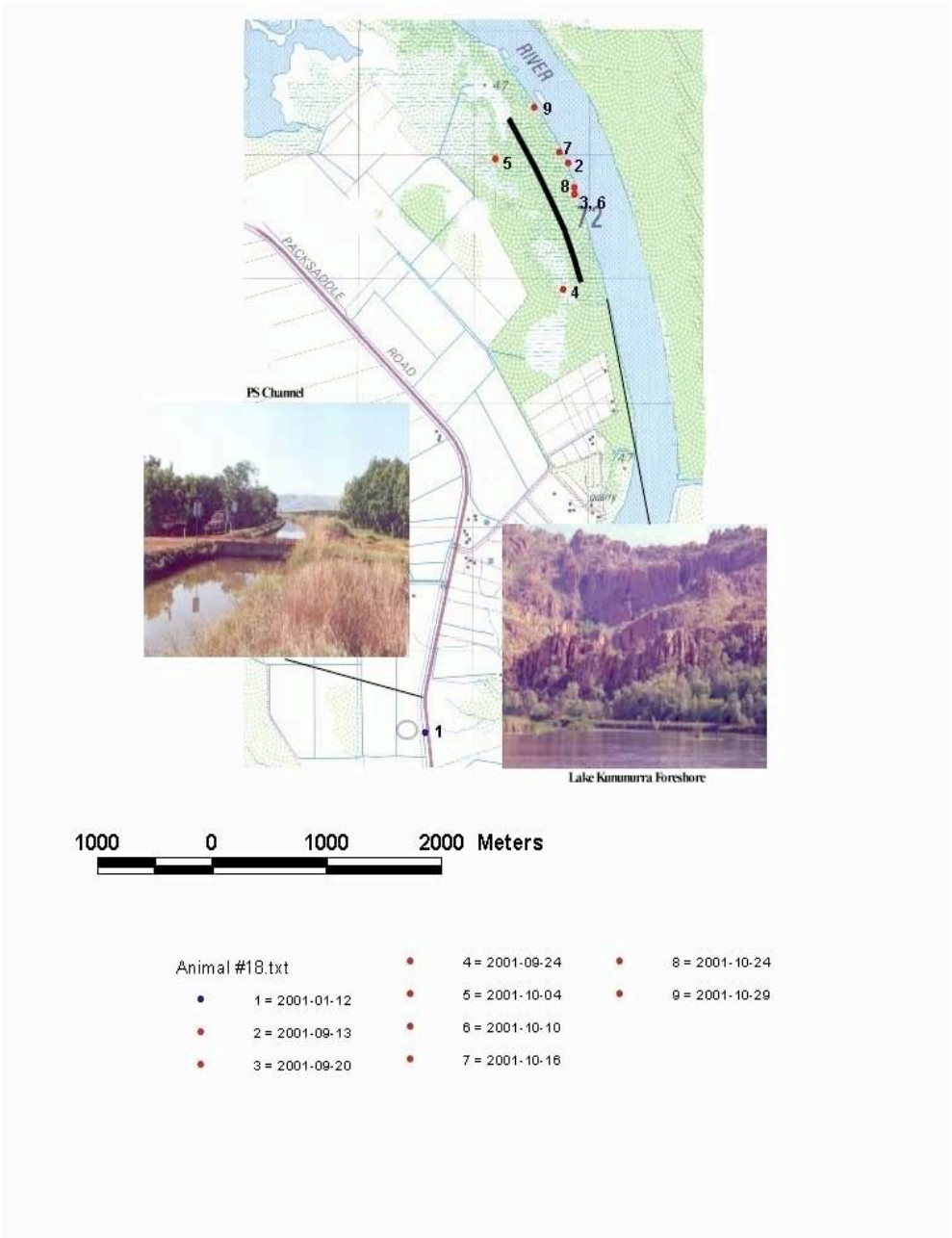


Figure 6.51: Left: Long-term movements of animal #2 (SVL = 420 mm, Sex = UC) in the IPM1and D1, outline indicates the position of a seasonal (wet season) swamp adjacent the IPM1. Above: Activity distance accumulated for each positional fix following release.

Table 6.51: Length, width and area of total activity areas and core activity areas (CAA).

Site	Total Length (m)	Width (m)	Area (m^2)	Length of CAA's (m)	Width (m)	Area (m^2)
Channel	2471	20	49420	105	20	2100
				92	20	1840

Long-term movements: Animal #2 used a section of the IPM1 and D2. It used two core activity areas both a section of the IPM1. It was only found outside these areas soon after capture and release on the 17/2/01 and subsequently on the 2/5/01. Animal #2 was not found after the 11/12/01.



Animal #18

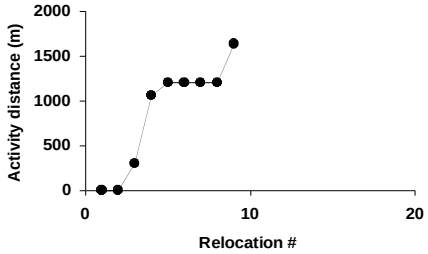
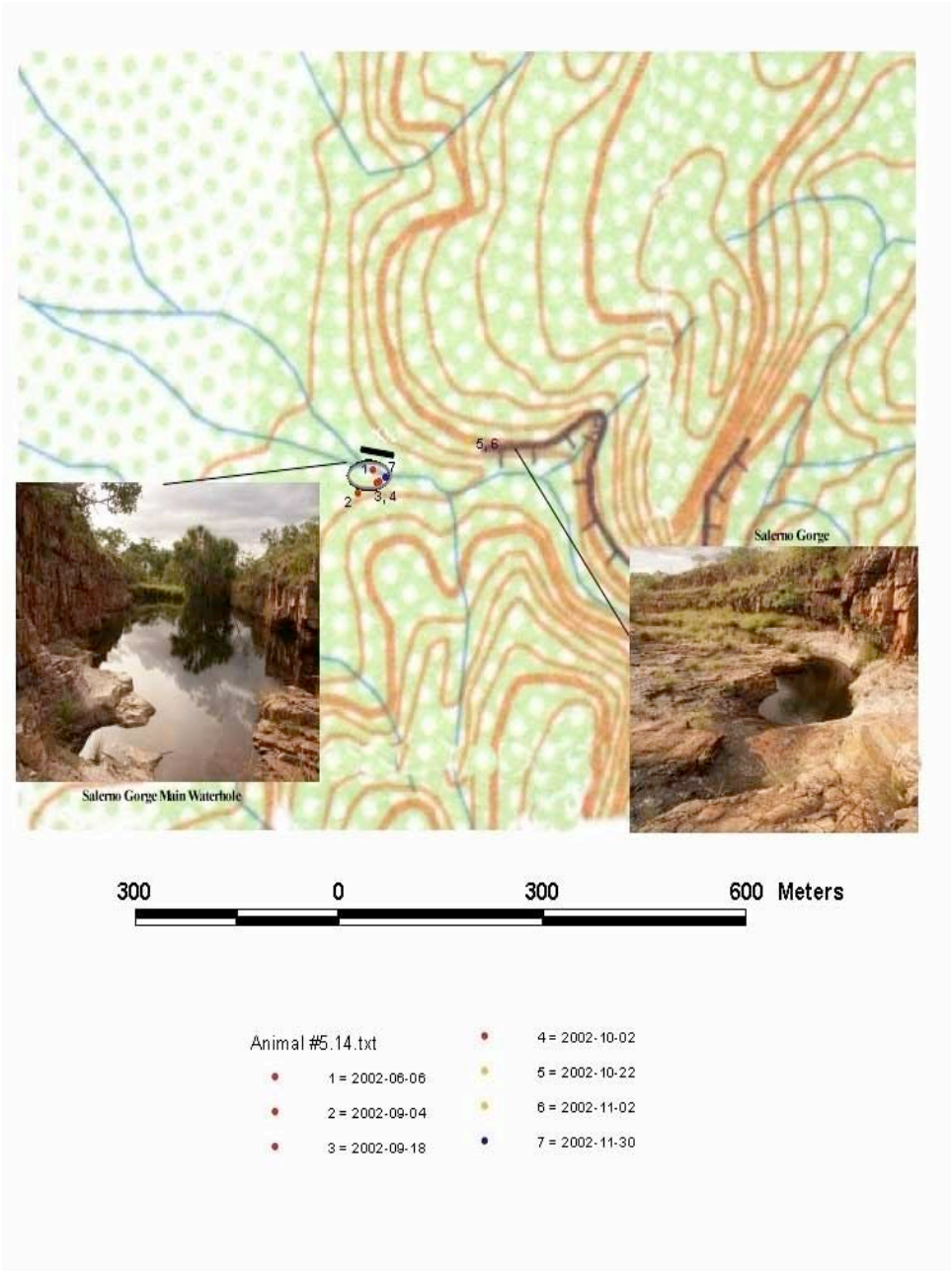


Figure 6.52: Left: Long-term movements of animal #18 (SVL = 450 mm, Sex = UC) along LKF, Circle indicates the position of farm dam 1 adjacent the PSMIC. Above: Activity distance accumulated for each subsequent positional fix following release.

Table 6.52: Length, width and area of total activity areas and core activity areas (CAA).

Site	Total Length (m)	Width (m)	Area (m^2)	Length of CAA's (m)	Width (m)	Area (m^2)
Lake foreshore	1638	100	163800	1638	100	163800

Long-term movements: Animal #18 used a length of the LKF. It used one core activity area a length of LKF. It was only found outside this area upon capture and release on the 12/1/01. Given animal #18 was not found in the PSMIC after release long-term movements only include movements along a length of LKF. Animal #18 was not found after the 29/10/01.



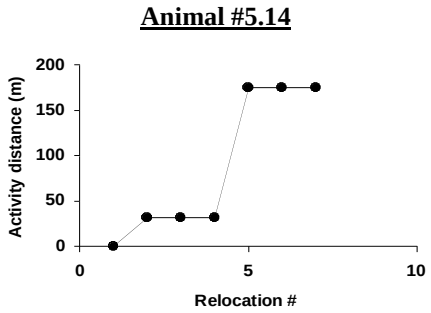


Figure 6.53: Left: Long-term movements of animal #5.14 (SVL = 380 mm, Sex = ♂) in the Salerno Gorge (SG), circle indicates the position of the SG waterhole. Areas used during all daily observations indicated in grey. Above: Activity distance accumulated for each subsequent positional fix following release.

Table 6.53: Length, width and area of total activity areas and core activity areas (CAA).

Site	Total length (m)	Width (m)	Area (m^2)	Diameter of CAA's (m)	Width (m)	Area (m^2)
Watercourse	175	30	5250	43		1452

Long-term movements: Animal #5.14 used a length of the SG including the Main Waterhole. It used one core activity area the main waterhole. It was only outside this area on the 22/10/02 and 2/11/02 when it was found burrowed and inactive east in SG. Following this period of inactivity it returned to its core activity area in the main waterhole. Animal #18 was not found after the 30/11/02.

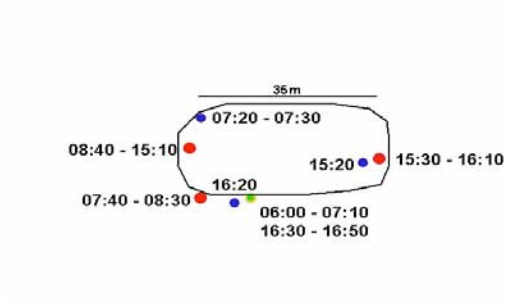


Figure 6.54: Daily movements of animal #5.14 in SG waterhole of SG on the 13/6/02.

Table 6.54: Areas where different behaviours were undertaken and their duration.

Behaviour	Time (mins)	Location
Basking	440	Rocks on waters edge
Swimming	10	Main pool
Walking	10	Rocks on waters edge

Daily movements: Included an area of the main waterhole with diameter 35 m and area 962 m². The individual remained in main waterhole throughout the day until it retreated into a burrow at 16:30 hrs where it remained until the observation day was terminated at 16:50 hrs. Distance moved 121 m equating to a speed of 0.25 m min^{-1}. One burrow location in rock crevice used both prior to emergence and after retreat.

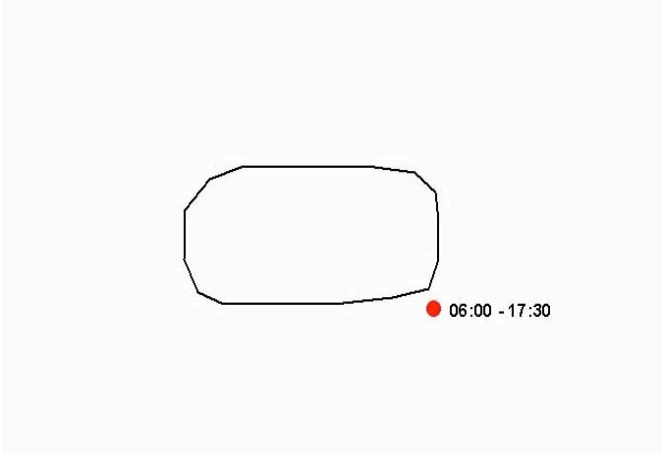


Figure 6.55: Daily movements of animal #5.14 in SG waterhole on the 14/6/02.

Table 6.55: Areas where different behaviours were undertaken and their duration.

Behaviour	Time (mins)	Location
Basking	520	Rock crevice

Daily movements: The individual remained basking on rocks outside its burrow entrance throughout day. One burrow in rock crevice approximately 5 m from waters edge used.

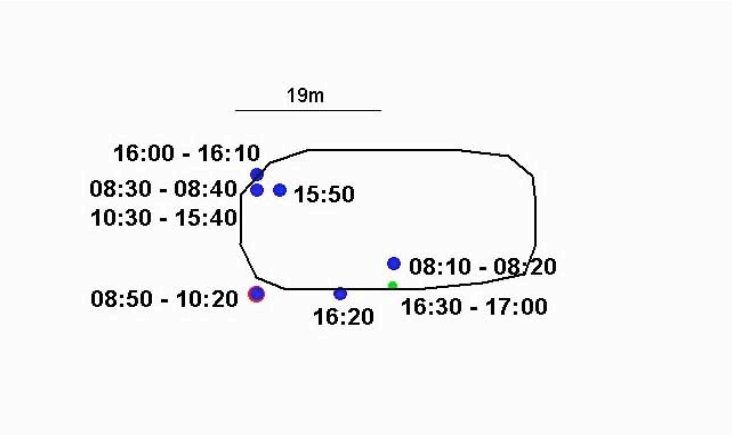


Figure 6.56: Daily movements of animal #5.14 in SG waterhole on the 2/7/02.

Table 6.56: Areas where different behaviours were undertaken and their duration.

Behaviour	Time (mins)	Location
Basking	70	Rocks on waters edge
Swimming	120	In main pool
Walking	30	Rocks on waters edge

Daily movements: Included an area of the main waterhole with diameter 19 m and area of 283 m². Individual remained in the main waterhole throughout the day. Distance moved 83 m equating to a speed of 0.16 m min^{-1}. No burrow locations observed being used.

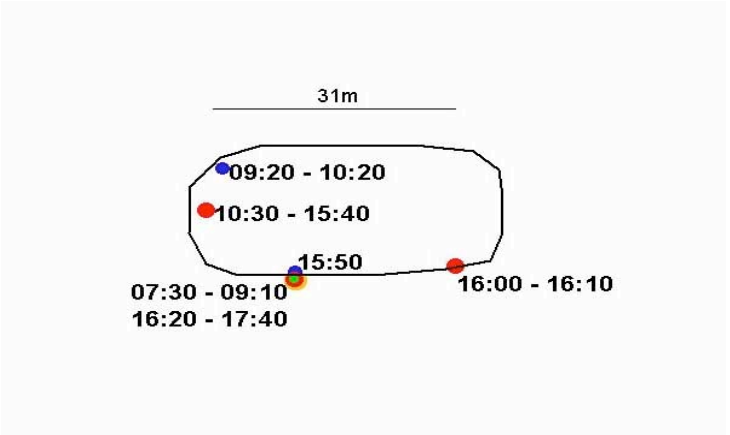


Figure 6.57: Daily movements of animal #5.14 in SG waterhole on the 31/7/02.

Table 6.57: Areas where different behaviours were undertaken and their duration.

Behaviour	Time (mins)	Location
Basking	360	Rocks on waters edge
Swimming	80	In main pool
Walking	10	Rocks on waters edge

Daily movements: Included an area of the main waterhole with diameter 31 m and area 754 m². Individual remained within main waterhole throughout the day until it retreated into a burrow at 16:20 hrs where it remained until the observation day was terminated at 17:40 hrs. Distance moved 83m equating to a speed of 0.16 m min^{-1}. One burrow used both before emergence and after retreat in a rock crevice.

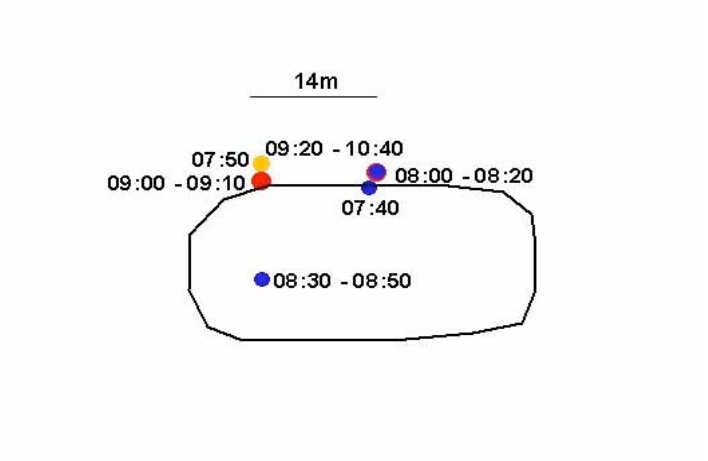


Figure 6.58: Daily movements of animal #5.14 in SG waterhole on the 30/11/02.

Table 6.58: Areas where different behaviours were undertaken and their duration.

Behaviour	Time (mins)	Location
Basking	40	Rocks on waters edge
Swimming	50	In main pool

Daily movements: Included an area of main waterhole with diameter 14 m and area 153 m². Individual remained within the main waterhole throughout day until it retreated into a burrow at 09:20 hrs where it remained until the observation day was terminated at 10:40 hrs. Distance moved 46 m equating to a speed of 0.42 m min^{-1}. One burrow in bank of main waterhole used both prior to emergence and upon retreat.

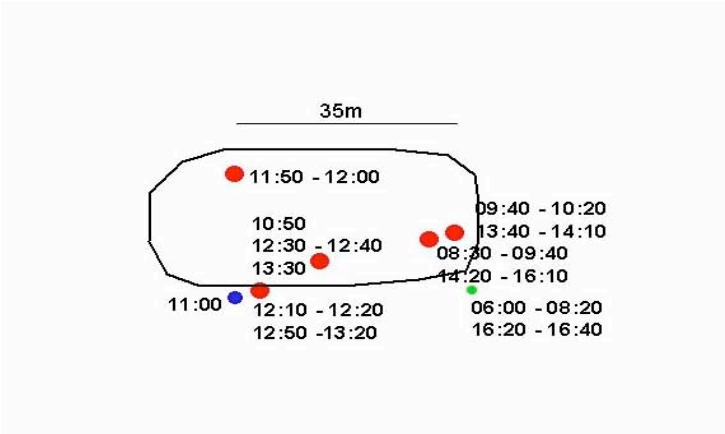
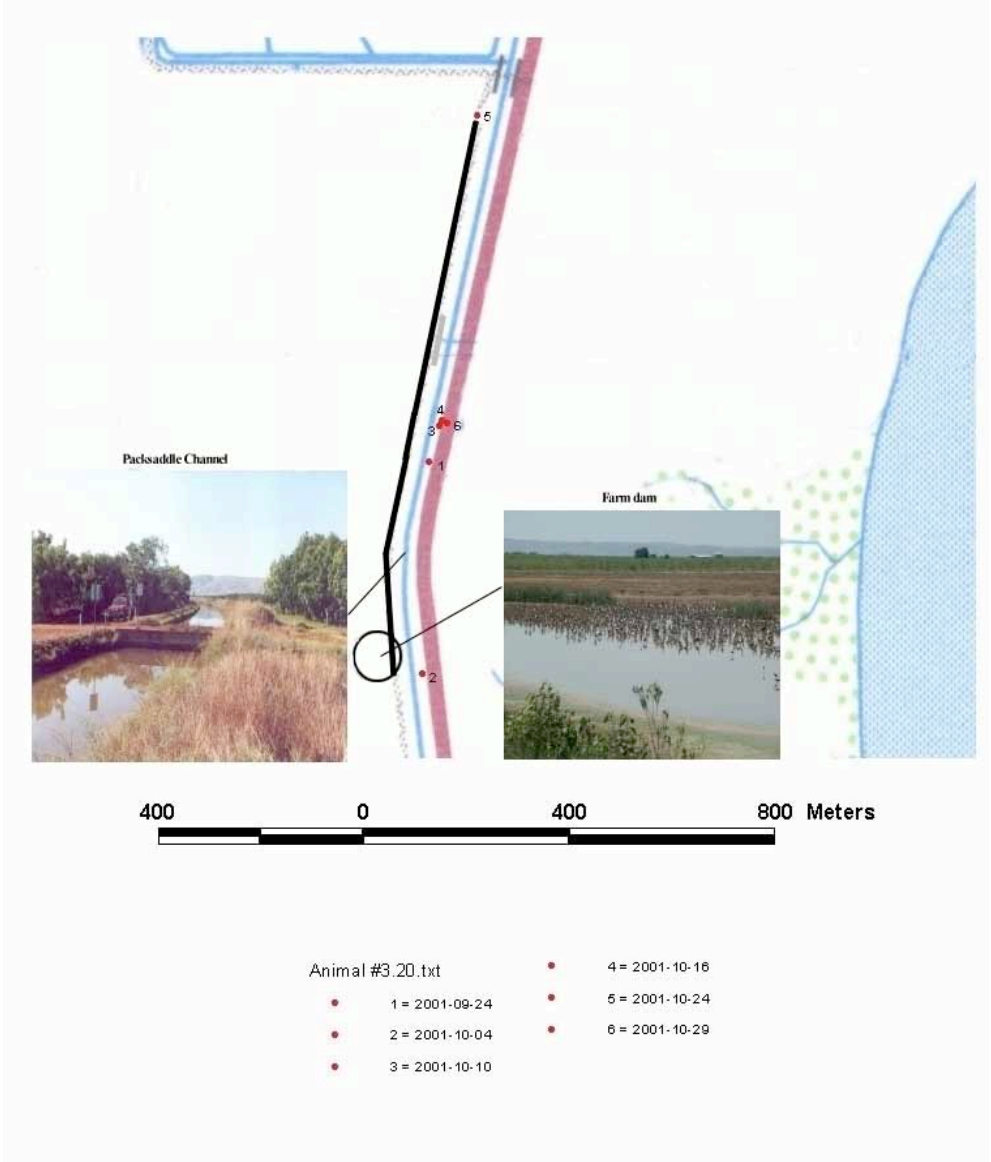


Figure 6.59: Daily movements of animal #5.14 in SG waterhole on the 1/8/03.

Table 6.59: Areas where different behaviours were undertaken and their duration.

Behaviour	Time (mins)	Location
Basking	500	Banks of waterhole
Swimming	40	In main pool
Walking	10	Banks of waterhole

Daily movements: Included an area of the main waterhole with diameter 35 m an area 962 m². Individual remained within the main waterhole throughout the day. Distance moved 104 m equating to a speed of 0.19 m min^{-1}. One burrow used both before emergence and after retreat in a rock crevice.



Animal #3.20

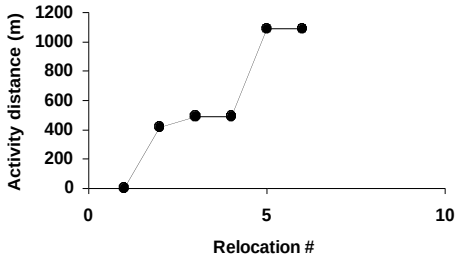


Figure 6.60: Left: Long-term movements of animal #3.20 (SVL = 400 mm, Sex = UC) in the PSMIC, circle indicates the position of farm dam 1 adjacent the PSMIC. Areas used during all daily observations also indicated (grey). Above: Activity distance accumulated for each subsequent positional fix following release.

Table 6.60: Length, width and area of total activity areas and core activity areas (CAA).

Site	Total Length (m)	Width (m)	Area (m^2)	Length of CAA's (m)	Width (m)	Area (m^2)
Channel	1090	10	10900	1090	10	10900

Long-term movements: Animal #3.20 used a length of the PSMIC. It used one core activity area a length of the PS channel. It was not found outside this area. Animal #3.20 was not found after the 29/10/01.

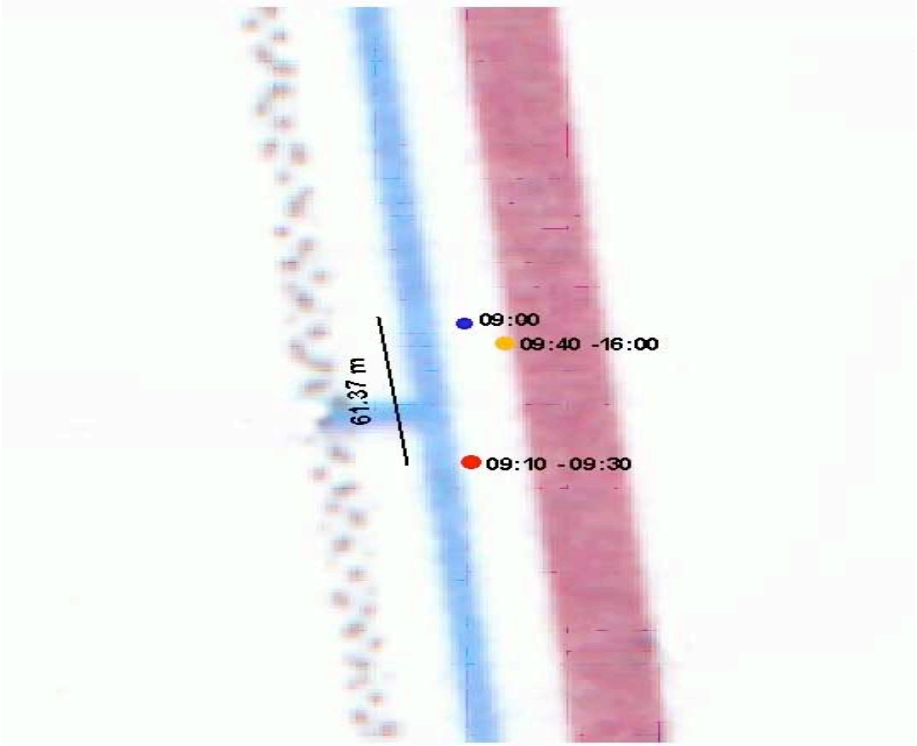
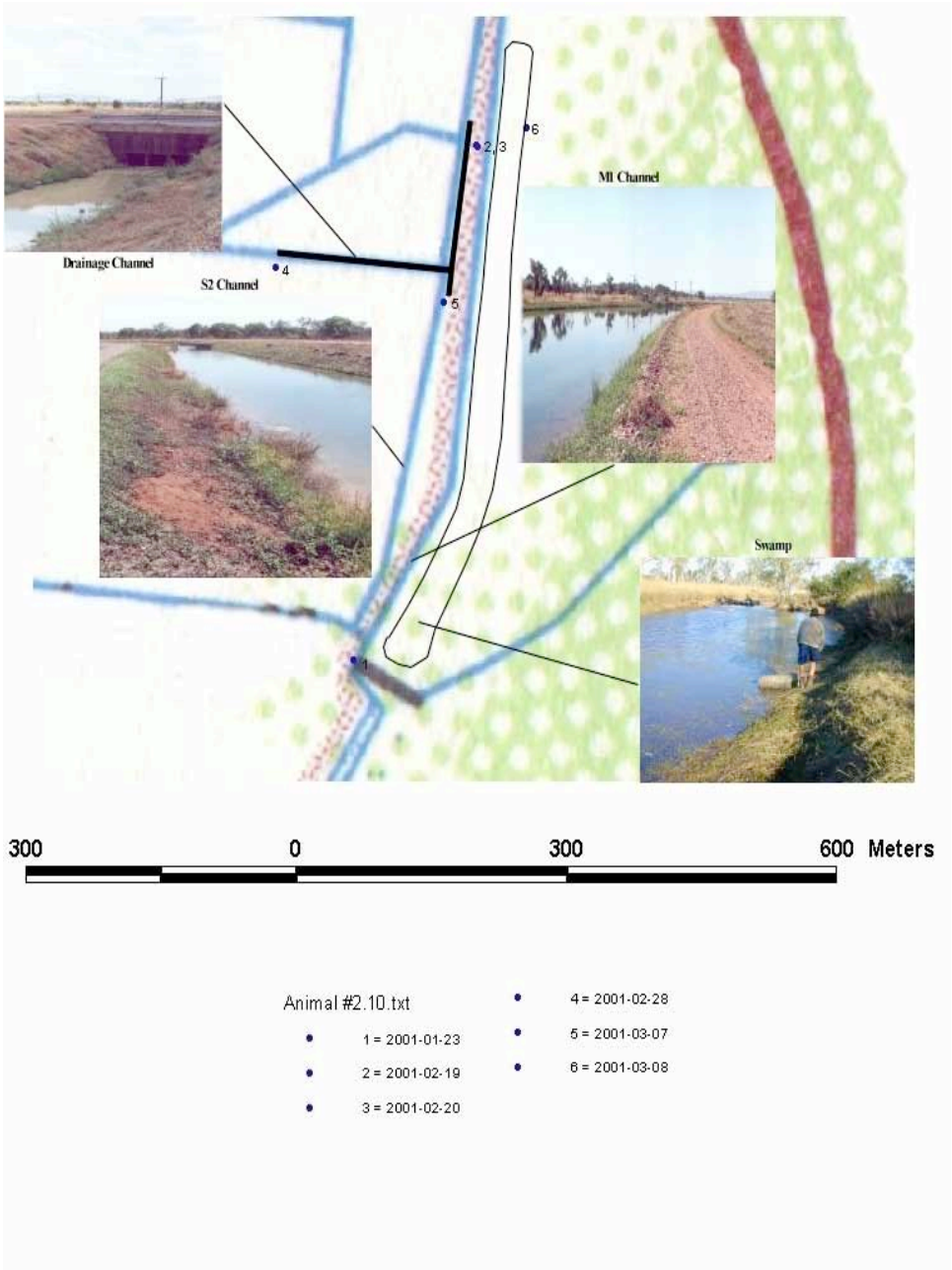


Figure 6.61: Left: Daily movements of animal #3.20 in the PSMIC on the 21/9/01.

Table 6.61: Areas where different behaviours were undertaken and their duration.

Behaviour	Time (mins)	Location
Basking	30	Banks of channel
Swimming	20	In channel

Daily movements: Included a section of the PSMIC length 61 m and area of 610 m². The individual remained in the PSMIC throughout the day until it retreated to a burrow at 09:40 hrs where it remained until the observation day was terminated at 16:00 hrs. Distance moved 107 m equating to a speed of 2.69 m min^{-1}. One burrow in bank of irrigation channel used upon retreat.



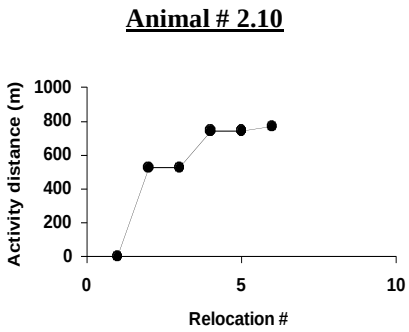
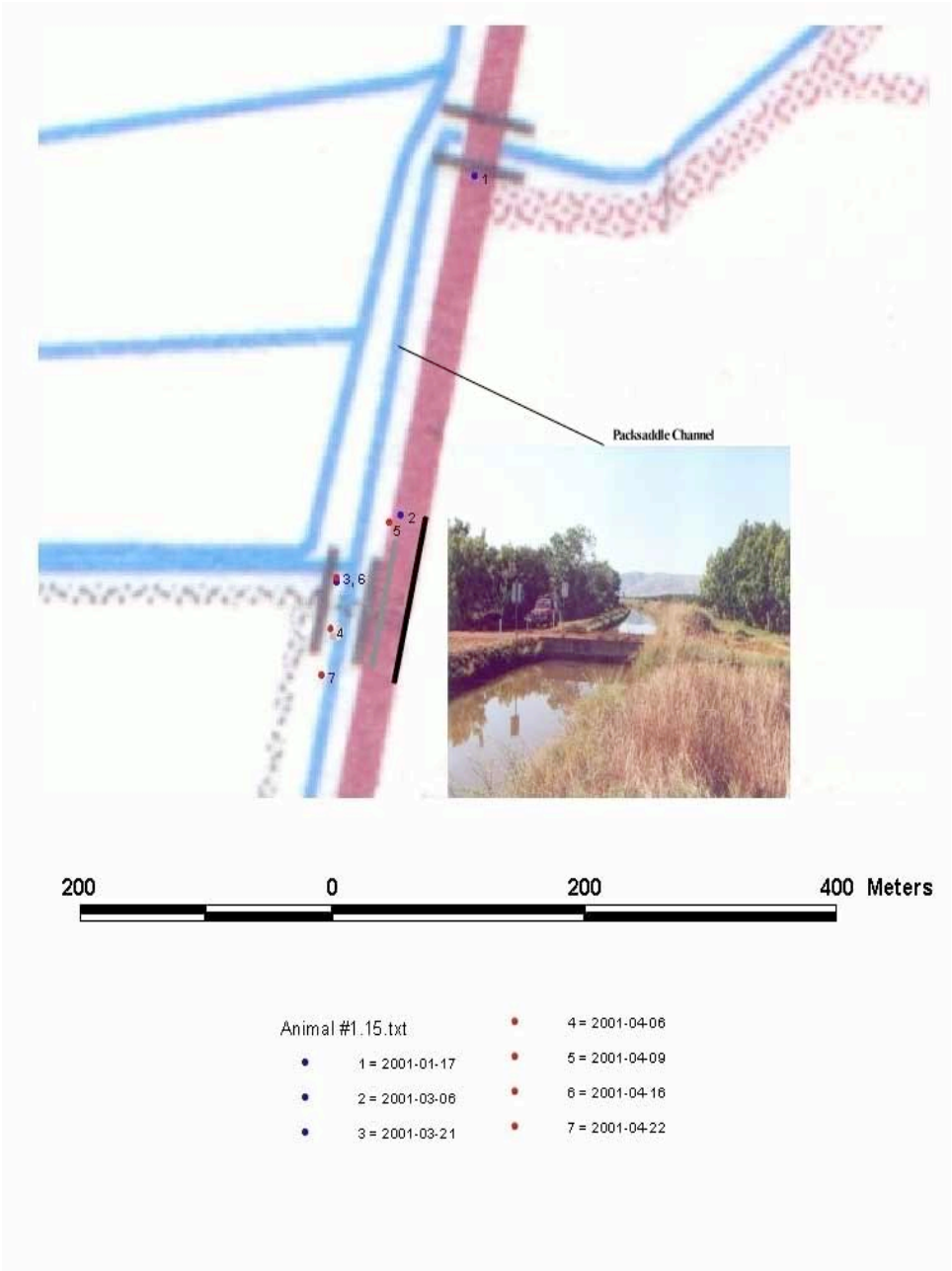


Figure 6.62: Left: Long-term movements of animal #2.10 (SVL = 380 mm, Sex = UC) in the IPM1, S2 and Drainage Channel, outline indicates the position of a seasonal (wet season) swamp adjacent IPM1. Above: Activity distance accumulated for each subsequent positional fix following release.

Table 6.62: Length, width and area of total activity areas and core activity areas (CAA).

Site	Total Length (m)	Width (m)	Area (m^2)	Length of CAA's (m)	Width (m)	Area (m^2)
Channels	770	50	38500	164	50	8200

Long-term movements: Animal #2.10 used a length of the IPM1, S2 and a Drainage channel. It used one core activity area a length of the channels. It was only found outside this area upon release on the 23/1/01. Animal #2.10 was not found after the 8/3/01.



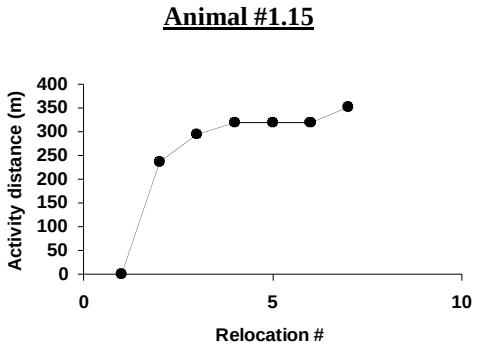


Figure 6.63: Left: Long-term movements of animal #1.15 (SVL = 390 mm, Sex = UC) in the PSMIC. Areas used during all daily observations also indicated (grey). Above: Activity distance accumulated for each subsequent positional fix following release.

Table 6.63: Length, width and area of total activity areas and core activity areas (CAA).

Site	Total Length (m)	Width (m)	Area (m^2)	Length of CAA's (m)	Width (m)	Area (m^2)
Channel	352	10	3520	120	10	1200

Long-term movements: Animal #1.15 used a length of the PSMIC. It used one core activity area a length of the PSMIC. It was only found outside this area upon capture and release on the 17/1/01. Animal #1.15 was not found after the 22/4/01.

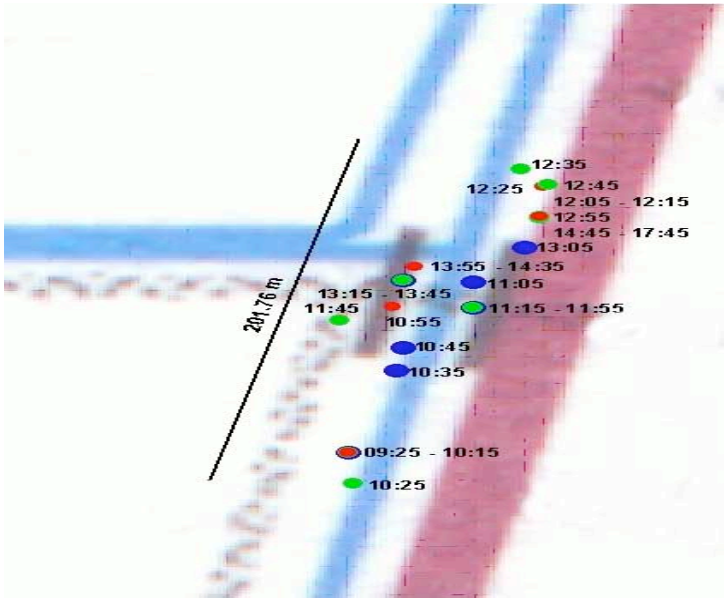
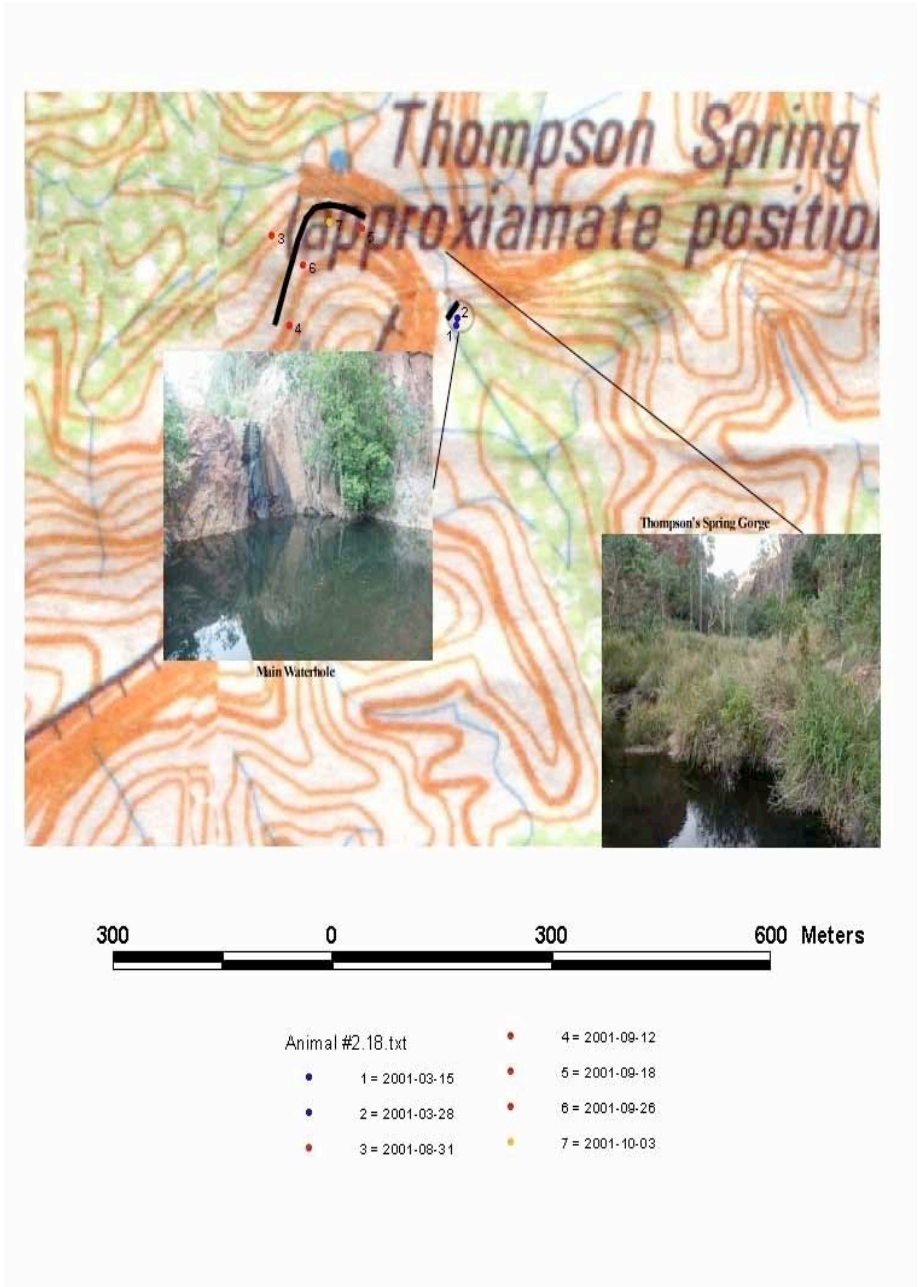


Figure 6.64: Left: Daily movements of animal #1.15 in PSMIC on the 18/4/01.

Table 6.64: Areas where different behaviours were undertaken and their duration.

Behaviour	Time (mins)	Location
Basking	280	Banks of channel
Swimming	90	In channel
Walking	130	Banks of channel/ access road

Daily movements: Included a section of irrigation channel length 201 m and area 2010 m². The individual remained in the PSMIC throughout the day. Distance moved 419 m equating to a speed of 0.84 m min^{-1}. No burrows observed being used.



Animal #2.18

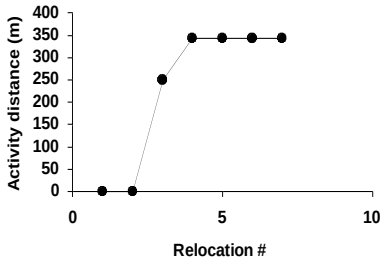


Figure 6.65: Left: Long-term movements of animal #2.18 (SVL = 450 mm, Sex = ♀) in the Thompson's Spring Gorge (TSG), circle indicates position of the main waterhole. Above: Activity distance accumulated for each subsequent positional fix following release.

Table 6.65: Length, width and area of total activity areas and core activity areas (CAA).

Site	Total Length (m)	Width (m)	Area (m^2)	Length/diameter of CAA's (m)	Width (m)	Area (m^2)
Watercourse	342	5	1710	210	5	1050
				18		254

Long-term movements: Animal #2.18 used a length of the TSG. It used two core activity areas one a section of TSG upstream of the main waterhole and the main waterhole. It was not found outside these areas. It was found burrowed and inactive in its western most core activity area on the 3/10/01. It was excavated to confirm inactivity status on the 2/8/01. Owing to this disturbance subsequent positional fixes of animal #2.18 were removed from analysis.

6.5.1 Daily activity distances and areas

Daily activity areas of individuals observed on different days varied considerably. For example animal #17, observed on 7 days, had daily activity areas ranging between 0.06 – 1.47 ha (Table 6.66).

The mean daily activity area of the five *V. mertensi* observed in irrigation watercourses was 0.66 ± 0.22 ha (Table 6.66). The mean daily activity area of animal #5.14 observed on five days in the main pool of Salerno Gorge was 0.07 ± 0.02 ha (Table 6.66).

The mean daily activity distance of the five *V. mertensi* along irrigation channels was 398.7 ± 88.09 m (Table 6.66). The mean diameter of dams used by two of these *V. mertensi* was 50.3 m (Table 6.66). The mean diameter of the main pool of Salerno Gorge used by animal #5.14 observed on five days was 24.5 ± 6.8 m (Table 6.66).

6.5.2 Use of daily activity areas

Repeated observations on different days were completed for three different *V. mertensi* (Table 6.2). Repeated observations of the same individuals on consecutive days showed individuals often use similar daily activity areas over several days (Figures 6.9, 6.10 and 6.16, 6.18 and 6.42, 6.43 and 6.54, 6.55, 6.57). Individuals also often subsequently returned to areas they had previously used (Figures 6.6, 6.7, 6.8, 6.9 and 6.13, 6.14 and 6.58, 6.59).

Table 6.66: The length of irrigation channels and diameter of farm dams and waterholes used by *V. mertensi* during their entire active day. Means ± SEM shown for both different observation days and different *V. mertensi*.

Animal	Date	Site	Length (m)	Diameter (m)	Channel activity area (ha)	Waterbody activity area (ha)	Combined activity area (ha)
1.7	31/01/2003	PSMIC	216.42		0.22		0.22
1.7	02/02/2003	Farm dam 2		40		0.12	0.12
1.7	29/01/2003	Farm dam 2		45		0.16	0.16
Mean				**42.5**		**0.14**	**0.17**
SEM							**0.03**
n (waterbodies)			**1**	**2**	**1**	**2**	**3**
n (days)			**3**	**3**	**3**	**3**	**3**
5.16	16/01/2003	IPM1	1102.13		2.20		2.20
5.16	20/01/2003	Swamp	55.76		0.02		0.02
Mean			**578.95**		**1.12**		**1.11**
n (waterbodies)			**2**	**0**	**2**	**0**	**2**
n (days)			**2**	**2**	**2**	**2**	**2**
1.15	18/04/2001	PSMIC	201.76		0.2		0.20
8	19/10/2001	IPM1	622.44		1.24		1.24
17	21/05/2002	PSMIC	391.76		0.39		0.39
17	19/04/2002	PSMIC + farm dam 1	596.64	76.16	0.6	0.45	1.05
17	05/02/2002	PSMIC	456.17		0.46		
		Farm dam 1 bank	50			0.025	0.48
17	18/06/2002	PSMIC + farm dam 1	398.06	15.96	0.4	0.02	0.4
17	23/07/2002	PS channel	28.27		0.03		
		Farm dam 1 bank	54			0.027	0.06
17	23/04/2002	PSMIC + farm dam 1	1015.04	76.16	1.015	0.45	1.47
17	28/04/2001	Farm dam 1		64.2		0.3	0.3
Mean			**373.7**	**58.1**	**0.5**	**0.2**	**0.6**
SEM			**119.2**	**14.3**	**0.1**	**0.09**	**0.19**
n (waterbodies)			**8**	**4**	**6**	**7**	**7**
n (days)			**7**	**7**	**7**	**7**	**7**
Mean		**Human-altered waterbodies**	**398.7**	**50.3**	**0.66**	**0.17**	**0.66**
SEM			**88.09**		**0.22**		**0.22**
n (lizards)			**5**	**2**	**5**	**2**	**5**
5.14	01/08/2002	SG waterhole		35.47		0.096	0.096
5.14	02/07/2002	SG waterhole		19.49		0.096	0.096
5.14	31/07/2002	SG waterhole		31.98		0.075	0.075
5.14	13/06/2002	SG waterhole		35.47		0.096	0.096
5.14	14/06/2002	SG waterhole		0		0	0
Mean		**Natural waterbodies**		**24.5**		**0.07**	**0.07**
SEM				**6.8**		**0.02**	**0.02**
n (waterbodies)				**5**		**5**	**5**
n (days)				**5**		**5**	**5**
n (lizards)				**1**		**1**	**1**

6.5.3 Speed of movement and distance moved

The speed of movement of individuals observed on different days varied (Table 6.67). For example, animal #17 observed on multiple days, moved with speeds ranging between 0.56 – 4.84 m min^{-1} and animal #5.14 with speeds ranging between 0.16 – 0.42 m min^{-1} (Table 6.67). The mean daily speed of movement of six *V. mertensi* was 1.4 ± 0.3 m min^{-1} (Table 6.67).

Individuals were also often observed moving rapidly between foraging areas during an active day. Rapid movement included either swimming or walking. The maximum speed at which an individual (animal #17) was observed moving was 14 m min^{-1} (Table 6.68). The maximum speed of movement of animal #17 on four different days showed variation between days (Table 6.68). Variation in the maximum speeds of two individuals (animals #17 and #8) also shows individual variation in maximum speeds of their movement (Table 6.68).

The mean distance moved by the six *V. mertensi* during an entire active day was 670 ± 270 m (Table 6.67). Distance moved during a day ranged from 0 – 2871 m (Table 6.67).

6.5.4 Daily behaviour

Six *V. mertensi* observed in irrigation watercourses spent 37 % of their total daily active time basking, 39 % swimming, 12 % foraging while swimming, 2 % foraging while walking, 9 % walking and 2 % not seen (Table 6.69). Animal #5.14 observed on six different days in the Salerno Gorge main waterhole spent 74 % of its total active time basking and 23 % swimming (Table 6.69).

Table 6.67: Total distance moved during an entire active day and daily speed of movement of six *V. mertensi*. Means ± SEM for both different observation days and different *V. mertensi* shown.

Animal	Date	Site	Total distance moved (m)	Speed (m min^{-1})
17	28/4/01	PSMIC	219.76	0.56
17	5/2/02	PSMIC	1098.22	2.11
17	19/4/02	PSMIC	1206.66	1.83
17	23/4/02	PSMIC	2758.67	4.84
17	21/5/02	PSMIC	530	0.77
17	18/6/02	PSMIC	477.73	0.78
17	23/7/02	PSMIC	310.43	0.57
Mean			943.07	1.64
SEM			334.54	0.58
N (days)			7	7
1.7	29/1/03	PSMIC	324.60	0.95
1.7	31/1/03	PSMIC	556.22	1.16
1.7	2/2/03	PSMIC	399	0.7
Mean			426.61	1.74
SEM			68.27	0.4
n (days)			3	3
8	19/10/01	IPM1	635.11	1.41
5.16	16/1/03	IPM1	2871.11	4.79
5.16	20/1/03	IPM1	181.72	0.31
Mean			1526.42	2.55
SEM			n.a	n.a
n (days)			2	2
1.15	18/4/01	PSMIC	419.40	0.84
5.14	13/6/02	SG waterhole	121.35	0.25
5.14	14/6/02	SG waterhole	0	0
5.14	2/7/02	SG waterhole	83.58	0.16
5.14	31/7/02	SG waterhole	46.47	0.42
5.14	1/8/03	SG waterhole	104.99	0.19
Mean			71.28	0.20
SEM			21.78	0.07
n (days)			5	5
Mean			**670.32**	**1.40**
SEM			**207.34**	**0.33**
N (lizards)			**6**	**6**

Table 6.68: Maximum speed of movement of two *V. mertensi* observed on different days. Distance moved, time period observed and minutes taken to move also shown.

Animal #	Date	Site	Distance moved (m)	Time (mins)	Speed (m min^{-1})
17	5/2/02	PSMIC	280	15:05 – 15:25 = 20	14
17	12/3/02	PSMIC	200	10:00 – 10:30 = 30	6.7
17	18/6/02	PSMIC	379	10:40 – 12:50 = 130	3
17	23/11/02	PSMIC	536	07:00 – 08:40 = 100	5.4
Mean			**348**		**7**
SEM			**72**		**2**
8	19/10/01	IPM1	270	09:05 – 10:55 = 110	2.5
8	10/12/01	IPM1	622	09:30 – 11:40 = 130	4.8
Mean			**446**		**3**

Table 6.69: Time spent behaving in different ways by seven *V. mertensi* and percentage of total time active spent behaving in different ways shown in parentheses. Mean percentage of total active time spent behaving in different ways for individuals observed on different days and different *V. mertensi* given.

Animal	Date	Site	Basking time (mins)	Swimming time (mins)	Foraging (swimming) time (mins)	Foraging (walking) time (mins)	Walking time (mins)	Not seen time (mins)	Total active time (mins)
17	28/4/01	PSMIC	110 (34.3)	130 (40.6)	0 (0)	0 (0)	80(25)	0 (0)	320
17	29/5/01	PSMIC	110 (35.4)	30 (9.7)	0 (0)	0 (0)	179 (54.8)	0 (0)	310
17	5/2/02	PSMIC	50 (9.6)	50 (9.6)	0 (0)	30 (5.7)	0 (0)	390 (75)	520
17	12/3/02	PSMIC	40 (11.4)	140 (40)	30 (8.5)	50 (14)	0 (0)	90 (25.7)	350
17	19/4/02	PSMIC	250 (39)	190 (29.7)	170 (26.5)	30 (4.6)	0 (0)	0 (0)	640
17	23/4/02	PSMIC	100 (19.2)	100 (19.2)	270 (51.9)	40 (7.6)	10 (1.9)	0 (0)	520
17	21/5/02	PSMIC	310 (66)	160 (34)	0 (0)	0 (0)	0 (0)	0 (0)	470
17	18/6/02	PSMIC	140 (37.8)	230 (62.1)	0 (0)	0 (0)	0 (0)	0 (0)	370
17	23/7/02	PSMIC	390 (70.9)	150 (27.3)	0 (0)	0 (0)	10 (1.8)	0 (0)	550
17	23/11/02	PSMIC	60 (23)	140 (53.8)	40 (15.4)	20 (7.6)	0 (0)	0 (0)	260
Mean			**34.7 %**	**32.6 %**	**10.2%**	**4%**	**8.4%**	**10.1 %**	
1.7	29/1/03	PSMIC	0 (0)	120 (35.3)	220 (64.7)	0 (0)	0 (0)	0 (0)	340
1.7	31/1/03	PSMIC	20 (4.1)	270 (56.3)	190 (39.5)	0 (0)	0 (0)	0 (0)	480
1.7	2/2/03	PSMIC	0 (0)	570 (100)	0 (0)	0 (0)	0 (0)	0 (0)	570
Mean			**1.4 %**	**63.9 %**	**34.7 %**	**0 %**	**0 %**	**0 %**	
8	19/10/01	IPM1	180 (54.5)	90 (27.3)	10 (3)	40 (12)	10 (3)	0 (0)	330
8	10/12/01	IPM1	70 (58.3)	10 (8.3)	20 (16.7)	0 (0)	20 (16.7)	0 (0)	120
Mean			**56.4 %**	**17.8 %**	**9.9%**	**6%**	**9.9 %**	**0 %**	
5.16	16/1/03	IPM1	130 (21.7)	250 (41.7)	180 (30)	10 (1.7)	30 (5)	0 (0)	600
5.16	20/1/03	IPM1	30 (5.1)	480 (82.8)	0 (0)	0 (0)	70 (12)	0 (0)	580
Mean			**13.4 %**	**62.3 %**	**15%**	**0.9%**	**8.5 %**	**0 %**	
3.20	21/9/01	PSMIC	30 (60)	20 (40)	0 (0)	0 (0)	0 (0)	0 (0)	50
1.15	18/4/01	PSMIC	280 (56)	90 (18)	0 (0)	0 (0)	130 (26)	0 (0)	500
Mean		**Human-altered waterbodies**	**37 %**	**39.%**	**12 %**	**2 %**	**9 %**	**2 %**	
n			**6**	**6**	**6**	**6**	**6**	**6**	
5.14	13/6/02	SG waterhole	440 (95.7)	10 (2.1)	0 (0)	0 (0)	10 (2.1)	0 (0)	460
5.14	14/6/02	SG waterhole	520 (100)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	520
5.14	2/7/02	SG waterhole	70 (31.8)	120 (54.5)	0 (0)	0 (0)	30 (13.6)	0 (0)	220
5.14	31/7/02	SG waterhole	360 (80)	80 (17.8)	0 (0)	0 (0)	10 (2.2)	0 (0)	450
5.14	30/11/02	SG waterhole	40 (44.4)	50 (55.5)	0 (0)	0 (0)	0 (0)	0 (0)	90
5.14	1/8/02	SG waterhole	500 (90.9)	40 (7.2)	0 (0)	0 (0)	10 (1.8)	0 (0)	550
Mean		**Natural waterbodies**	**74 %**	**23 %**	**0 %**	**0 %**	**3 %**	**0 %**	
n			**1**	**1**	**1**	**1**	**1**	**1**	

6.5.5 Burrow locations

Overnight refuge burrows were predominantly located on the water's edge. Burrows were located in the banks of irrigation channels, farm dams, and waterholes and in rock crevices close to the water's edge. Generally individuals retreated into their burrows late in the afternoon without travelling a substantial distance just prior to retreat. On two occasions, however, individuals were observed returning to a burrow after moving a distance of approximately 500 m just prior to retreat. An individual moved approximately 500 m in 100 minutes between 15:10 and 16:50 hrs (Figure 6.42) and another in 30 minutes between 16:35 and 17:05 hrs (Figure 6.10). On 10 observation days individuals were observed both emerging and retreating to burrows. On six of these occasions individuals retreated to the same burrow from which they emerged (Figures 6.17, 6.43, 6.54, 6.57, 6.58 and 6.59). On the other four occasions individuals retreated to a different burrow from which they emerged (Figures 6.9, 6.10, 6.17, 6.42).

6.5.6 Burrow size and shape

A total of 27 overnight refuge burrows confirmed as being used by *V. mertensi* were probed and measured. Of these, six burrows were measured at natural water-bodies such as creek lines (n = 4) and waterholes (n = 2). Twenty one burrows were measured within irrigation area watercourses such as Lake Kununurra (n = 1), farm dams (n = 2) and irrigation channels (n = 18). The mean height of burrow entrances above the water level was 11.1 ± 2.7 cm (n = 24). Eleven (40%) of the burrows examined had entrances on the high water level of their respective water-bodies. The mean height of burrow entrances was 9.7 ± 1 cm (n = 27) and width of entrances was 15.5 ± 1 (n = 27). The mean length of burrows was 131.4 ± 13.1 cm (n = 27). The shape of burrow entrances was flat bottomed with an arched roof (Plate 6.2, page 184).

The shape profile of 20 (74.07%) burrows probed was straight with a gentle upward slope. Five (18.5%) of the burrows had a bent shape, either bending to the right or left with a gentle upward slope. Two (7%) burrows had a shape dictated by cracks in rock surfaces in which they were located. Only one burrow was found to have a second entrance located approximately 1 m up the bank of an irrigation channel from the water level entrance to the burrow.

6.5.7 Basking sites

In total 81 basking sites were used by *V. mertensi* during observation days. Only one basking site was located (approximately 10 m) away from the water's edge, just outside an overnight refuge burrow in a rock crevice (Figure 6.55). All other basking sites were on mud banks, rocks, roads and irrigation structures close to the waters edge. On several occasions *V. mertensi* were also observed basking on top of floating weed in waterbodies. All behaviour categorised as basking was undertaken at locations exposed to direct sunlight. *Varanus mertensi* was not observed displaying basking behaviour in the shade.

6.5.8 Foraging areas

Individuals were not observed foraging more than approximately 5 metres away from the water's edge. Areas foraged included; in the water (along the benthos and in the water column), along the bank of waterbodies, amongst riparian vegetation and along roads adjoining irrigation channels. Individuals often concentrated their foraging along the bank/water interface on the edge of waterbodies (Plate 6.3). Detailed observations of foraging sequences also showed *V. mertensi* forage while swimming through the water column or along the benthos and (or) walking through riparian vegetation bordering watercourses (Chapter 4). These observations also showed that foraging *V. mertensi* concentrate their efforts along the bank/water interface of waterbodies (Chapter 4).

Plate 6.2: The 'typical' entrance shape and location of a *V. mertensi* refuge burrow on high water mark of an irrigation channel.

Plate 6.3: A *V. mertensi* foraging along the bank/water interface of the Main Irrigation Channel of the Ivanhoe Plains Irrigation Area.

6.5.9 Long-term movement patterns

Numerous *V. mertensi* were subsequently located a substantial distance away from their point of capture and release following handling and surgical implantation of radio-transmitters (Figures 6.19, 6.20, 6.36, 6.37, 6.47, 6.50, 6.51, 6.52, 6.62 and 6.63).

The long-term movements of 37 radio-tagged *V. mertensi* resembled the shape of watercourses in which each individual was found (Figures 6.4 - 6.65). For individuals found in irrigation areas this included irrigation channels, swamps, Lake Kununurra and farm dams within the ORIS. For individuals found in natural watercourses this included creeks and waterholes. During the field study no positional fix of a *V. mertensi* was recorded a substantial distance from water. In several cases individuals were found to have moved between spatially separated waterbodies e.g. between Packsaddle Main Irrigation Channel and the Lake Kununurra Foreshore. It is unclear how individuals moved between these waterbodies. It is possible that they moved through the terrestrial environment between these waterbodies (Figures 6.4, 6.15, 6.25), as they moved into Lake Kununurra from the Packsaddle Plains Main Irrigation Channel and along the Lake Kununurra Foreshore (Figures 6.4, 6.15, 6.25). The findings of this study are inconclusive in this area.

All radio-tagged *V. mertensi* were identified using at least one core activity area within their long-term activity areas (Table 6.71, page 188). Numerous individuals were found to move between core activity areas (Figures 6.4, 6.15, 6.21, 6.23, 6.24, 6.25, 6.27, 6.44, 6.45, 6.51 and 6.65). Some individuals were also found to move between core activity areas on a seasonal basis. For example, animals #17, 1.7 and 6 moved between the same core activity areas at similar times during consecutive years (Figures 6.4, 6.15 and 6.23). Individuals often moved large distances in search of new core activity areas (Figures 6.23; fixes 31-32 and 41-42, 6.24; fixes 47-48, 6.24; fixes 36-38 and 44-45, 6.44; fixes 5-12, 6.42; fixes 9-10, 6.47; fixes 12-13, 6.48; fixes 10-11 and 6.65; fixes 3-7).

Twenty one percent of radio-tagged *V. mertensi* were found to burrow and remain inactive for varying lengths of time. The details of this behaviour and the characteristics of core activity areas are outlined in the following sections.

6.5.10 Activity areas

The long-term activity areas of 32 *V. mertensi* found in irrigation waterbodies ranged between 0.03 – 31.8 ha and five found in natural waterbodies between 0.005 – 0.05 ha (Table 6.71, page 188).

6.5.11 Activity area and body size

There was no significant effect of body mass on the size of activity areas of 31 *V. mertensi* for which > 10 positional fixes were recorded during the field study (r^2 = 0.04, $F_{1,30}$ = 1.175, ns). Snout-vent length also had no significant effect on activity area size (r^2 = 0.01, $F_{1,30}$ = 0.234, ns) (Figure 6.66; Table 6.70).

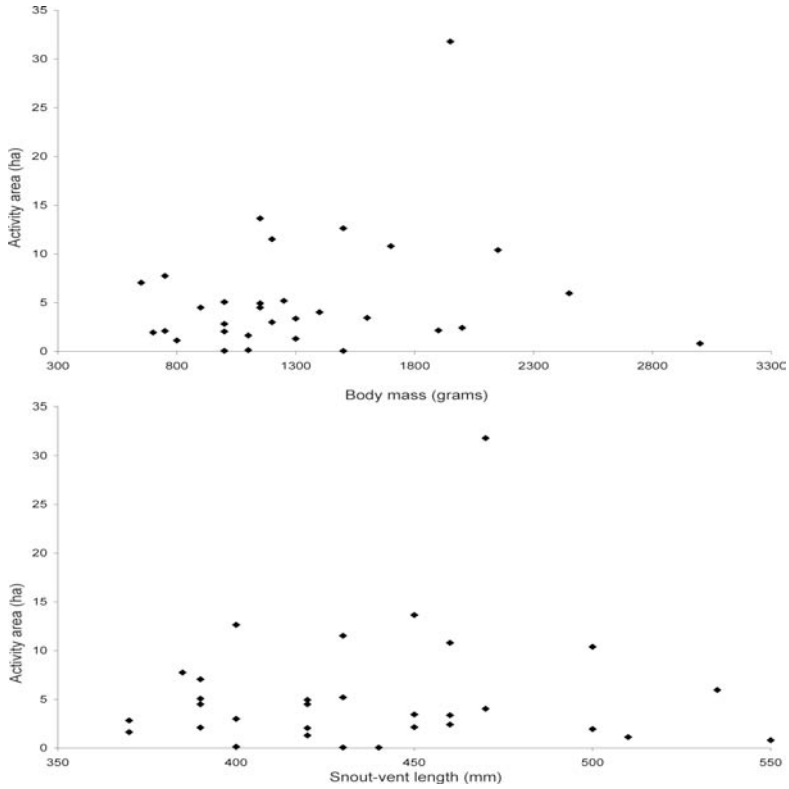


Figure 6.66: The relationship between body mass and activity area (top) and snout-vent length and activity area (bottom) of 31 *V. mertensi* for which > 10 positional fixes were recorded during the field study.

6.5.12 Activity areas of males and females

The mean activity area of male *V. mertensi* for which > 10 positional fixes were recorded was 8.98 ± 4.74 ha (n = 6) (Table 6.70). The mean activity area of females was 3.4 ± 1.5 ha (n = 4) (Table 6.70). Unfortunately this sample size for males prevents a meaningful statistical analysis of this data.

6.5.13 Core activity areas

The 32 *V. mertensi* found in irrigation waterbodies were identified using a minimum of 45 core activity areas (Table 6.71). The number of core activity areas used by individuals ranged from one (n = 20) to three (n =3). The size of core activity areas ranged between 0.03 – 16.8 ha (Table 6.71). Five *V. mertensi* found in natural waterbodies were identified using a minimum of 6 core activity areas. The number of core activity areas used by individuals ranged between one (n = 4) and two (n = 1). The size of core activity areas ranged between 0.03 – 0.15 ha (Table 6.71).

Table 6.70: The body mass and activity areas of 31 *V. mertensi* for which > 10 positional fixes were recorded. Location where individuals were found, sex of individuals and number of positional fixes recorded also given.

Animal #	Location	Body mass (grams)	SVL (mm)	Sex	# positional fixes	Duration	Activity area (ha)
17	PSMIC/ LKF	1000	370	unconfirmed	82	12/1/01-28/1/03	2.83
1.7	PSMIC/ LKF	1250	430	"	90	13/1/01-30/1/03	5.2
15	IPM1	1200	430	"	28	12/1/01-12/2/02	11.52
5	"	1400	470	"	27	10/1/01-10/9/01	4.03
1	IPM1/ S2	2450	535	"	47	12/1/01-12/2/02	5.96
12	"	650	390	"	42	11/1/01-22/3/02	7.06
6	IPM1/LKF	750	390	"	42	9/1/01-27/5/02	2.1
1.8	"	1000	420	"	40	14/1/01-15/10/02	2.05
1.16	PSMIC/ LKF	1600	450	"	79	17/1/01-28/1/03	3.45
11	IPM1	1500	400	unconfirmed	59	11/1/01-15/5/02	12.64
1.13	"	1300	420	♀	49	16/1/01-4/2/02	1.3
7	"	1950	470	♂	49	10/1/01-17/4/02	31.8
8	"	2150	500	♂	42	10/1/01-10/7/02	10.4
20	"	1150	420	unconfirmed	35	13/1/01-17/6/02	4.5
1.14	"	900	390	♂	35	16/1/01-17/9/01	4.5
4.9	"	2000	460	♀	28	24/7/01-24/2/02	2.42
2.6	"	800	510	unconfirmed	23	16/2/01-17/7/01	1.13
2.8	PSMIC	1000	390	unconfirmed	22	20/1/01-20/9/01	5.07
2.13	IPM1	700	500	♀	21	15/2/01-27/11/01	1.95
16	IPM1/S2	1700	460	unconfirmed	18	12/1/01-5/6/01	10.8
4.16	IPM1	1100	370	♂	17	14/11/01-4/7/02	1.64
4	IPM1/S2	1150	450	unconfirmed	16	9/1/01-29/1/02	13.65
5.16	IPM1	1200	400	unconfirmed	14	19/8/01-25/1/03	3
4.11	"	3000	550	unconfirmed	13	26/7/01-27/5/02	0.81
4.14	"	1900	450	♂	13	10/9/01-11/12/01	2.15
3.14	FMC	1100	400	unconfirmed	13	25/7/01-21/11/01	0.13
1.9	IPM1	750	385	♀	12	14/1/01-30/3/03	7.75
4.6	ACW	1500	440	unconfirmed	12	16/6/01-31/10/01	0.05
3.18	"	1000	430	unconfirmed	11	10/6/01-20/10/01	0.06
5.18	IPM1/S2	1300	460	♂	11	3/10/02-23/1/03	3.37
2	IPM1	1150	420	unconfirmed	11	9/1/01-11/12/01	4.94
Mean (♂)		**1550**	**440**		**27.8**		**8.98**
SEM		**210.6**	**20.33**		**6.6**		**4.74**
n		**6**	**6**		**6**		**6**
Mean (♀)		**1187.5**	**441.3**		**27.5**		**3.4**
SEM		**303.02**	**24.9**		**7.9**		**1.5**
n		**4**	**4**		**4**		**4**

Table 6.71: Length and area of long-term activity areas of 37 *V. mertensi*. The size of the smallest and largest areas are also shown. Minimum number of core activity areas, their length and area. The size of smallest and largest core activity areas also shown. # = animal number.

#	Activity area length/diameter (m)	Activity area (ha)	Minimum # of CAA	CAA length/diameter (m)	CAA area (ha)
17	Channel = 1686	1.69		Channel = 1686	1.97
	Dam = 76	0.45		Foreshore = 688	0.69
	Foreshore = 688	0.69		Dam = 76	0.45
	Total	**2.83**	3		
1.7	Channel = 4870	4.87		Channel = 3373	3.3
	Channel = 60	0.03		Channel = 60	0.03
	Dam = 30	0.28		Dam = 30	0.28
	Total	**5.2**	3		
15	Channel/swamp = 1152	11.52	1	Channel/swamp = 460	4.6
5	Channel = 2014	4.03	1	Channel = 708	14.12
1	Channel = 2978	5.96	2	Channel = 110	0.11
				Channel = 710	1.4
12	Channel = 1412	7.06	1	Channel = 950	4.7
6	Channel = 1006	2.0	2	Channel = 950	1.9
	Foreshore = 28	0.03		Inlet = 30	0.03
	Total	**2.1**			
1.8	Channel = 1006	2.02	2	Channel = 905	1.8
	Inlet = 25	0.03		Inlet = 25	0.03
	Total	**2.05**			
1.16	Channel = 2815	2.82	3	Foreshore = 631	0.63
	Foreshore = 631	0.63		Channel = 546	0.55
	Total	**3.45**		Channel = 2312	2.3
11	Channel/swamp = 1264	12.64	1	Channel/swamp = 1264	12.64
1.13	Channel = 652	1.30	2	Channel = 356	0.7
				Swamp = 82	0.4
7	Channels + swamp = 3186	31.8	1	Channels + swamp = 1375	13.7
8	Channels + swamp = 1039	10.4	1	Channels + swamp = 1039	10.4
20	Channel = 2248	4.5	1	Channel = 1380	2.7
1.14	Channel = 2248	4.5	1	Channel = 2248	4.5
4.9	Channel = 1210	2.42	1	Channel = 893	1.8
2.6	Channel = 565	1.13	1	Channel = 85	0.17
2.8	Channel = 5070	5.07	1	Channel = 1240	1.2
2.13	Channel = 976	1.95	1	Channel = 166	0.33
16	Channel/swamp = 1075	10.8	1	Channels/swamp = 1075	10.8
4.16	Channels = 820	1.64	1	Channels = 312	0.62
4	Channels + swamp = 1365	13.65	1	Channels + swamp = 473	4.7
5.16	Channel = 1510	3	1	Channel = 202	0.1
4.11	Channel = 402	0.80	2	Channel = 30	0.06
				Channel = 270	0.54
4.14	Channel = 1076	2.15	2	Channel = 335	0.67
				Channel = 261	0.52
1.9	Channel = 3876	7.75	1	Channel = 290	0.29
5.18	Channels + swamp = 337	3.37	1	Channels + swamp =235	2.35
2	Channel = 2471	4.94	2	Channel = 105	0.21
				Channel = 92	0.18
3.20	Channel = 1090	1.09	1	Channel = 1090	1.09
18	Foreshore = 1638	16.38	1	Foreshore = 1638	16.38
2.10	Channel = 770	3.85	1	Channels = 164	0.82
1.15	Channel = 352	0.35	1	Channel = 120	0.12
	Human-altered				
Min		**0.352**	**1**		**0.03**
Max		**31.8**	**3**		**16.38**
2.18	Watercourse = 342	0.17	2	Watercourse = 210	0.11
				Waterhole = 18	0.03
3.14	Watercourse = 260	0.13	1	Watercourse = 59	0.03
4.6	Waterhole = 26	0.053	1	Waterhole = 26	0.05
3.18	Waterhole = 28	0.062	1	Waterhole = 28	0.06
5.14	Watercourse = 175	0.53	1	Waterhole = 43	0.15
	Natural				
Min		**0.05**	**1**		**0.03**
Max		**0.5**	**2**		**0.15**

6.5.14 Mating season movements of different sexes

The sexes of 10 radio-tagged adult *V. mertensi* (6 males and 4 females) were confirmed through both hemipenile eversion and blood plasma sampling (Chapter 5). The movements of all males during the mating months of December, January and February were more extensive when compared to movements outside this period (Table 6.72). Additionally, two males moved to unknown locations during these months. Interestingly, the movements of all females also all showed differences during mating season months (Table 6.72).

Table 6.72: The movements of six male and four female *V. mertensi* during the mating season months of December – February. Only movements of adults with sex confirmed through both hemipenile eversion and blood plasma analysis shown.

#	Sex	Movement	Figure
7	♂	Moved more extensively north and south along M1 and into drain	6.28
8	♂	Moved more extensively north along M1 before moving to a unknown location	6.29
1.14	♂	Moved more extensively north along M1	6.33
4.16	♂	Moved more extensively both north and south along M1 and D1	6.39
4.14	♂	Moved more extensively north along M1 before moving to an unknown location	6.45
5.18	♂	Moved from M1 and swamp west to S2	6.50
4.9	♀	Moved more extensively both south and north along M1	6.34
2.13	♀	Moved more extensively south along M1	6.37
1.13	♀	Moved into a swamp and more extensively north along S2	6.27
1.9	♀	Moved into M1 and moved south along M1	6.47

6.5.15 Inactivity periods, burrow locations and water availability

Eight (21%) out of 37 radio-tagged *V. mertensi* burrowed and became inactive for a period of greater than one week. Individuals found in both irrigation areas and at three natural water-body sites; Thompson's Spring, Salerno Gorge and Four Mile Creek Gorge displayed inactivity (Table 6.73). Animal #17 became inactive for two extended periods in consecutive years at the same location (Figure 6.4, page 126). Animal #2.18 also was found inactive a second time on the 31/10/01, after first being exhumed while burrowed and inactive on the 2/8/01 (Figure 6.65, page 176.

All inactive individuals remained underground. The underground locations of inactive individuals were within 5 m of a nearby waterbody in all instances. There was no link between an absence of water and inactivity at any of the three natural

waterbody sites given all three waterbodies contained water year-round (pers.obs). Inactivity in irrigation areas was also not correlated with an absence of water. For example, the entire PSMIC was only shut down and drained on one occasion between the 9/10/01 and 20/11/01. However, several sections of the multiple section PSMIC were drained at other times including; section 1; between 6/1/02 - 22/1/02 and 24/2/02 - 5/3/02, section 2; between 24/12/01 - 6/1/02 and 24/2/02 - 5/3/02, and section 3; between 15/3/01 - 21/3/01 and 19/11/02 - 20/1/03. Despite these section shutdowns no one period corresponded directly with the commencement of inactivity by animal #17 between the 1/8/01 – 4/10/01 and the 14/5/02 -17/9/02.

The entire IPM1 was only shut down and drained of water on two occasions between the 13/3/01 - 15/3/01 and 20/3/01 - 23/3/01. However, several sections of the multiple section IPM1 were drained at other times including; section 1; between 27/3/01 - 29/3/01, section 2; between 13/3/01 - 5/4/01, 14/11/01 - 19/11/01, 11/12/01 - 14/1/02, 4/2/02 - 5/3/02, section 3; between 20/3/01 - 7/4/01, 14/11/01 - 5/12/01, 6/1/01 - 4/2/02, 24/2/02 - 13/3/02. Like the PSMIC, these section shutdowns did not directly correspond with the commencement of inactivity by animals #5, 1, 20 and 1.14 (Table 6.73). Although not correlated with an absence of water, inactivity was seasonal. Inactivity by *V. mertensi* at all locations only occurred during dry season months between May and October (Table 6.73).

Table 6.73: Duration, burrow location and figure showing long-term movement of eight *V. mertensi* found to burrow and become inactive for extended periods during the field study.

Animal #	Inactivity period	Burrow location	Figure
17	1/8/01 – 4/10/01	PS Pumphouse	6.4
17	14/5/02 – 17/9/02	PS Pumphouse	6.4
5	12/6/01 – 24/7/01	M1	6.20
1	9/7/01 – 6/8/01	S2	6.21
20	31/5/01 – 26/6/01	M1	6.32
1.14	12/6/01 – 9/7/01	M1	6.33
3.14	19/9/01 – 31/10/01	Four Mile Creek Gorge	6.47
5.14	22/10/02 – 2/11/02	Salerno Gorge	6.53
2.18	3/10/01 -	Thompson's Spring	6.65

6.5.16 Co-existence of *V. mertensi* individuals

The long-term activity areas of radio-tagged adult *V. mertensi* overlapped in both irrigation waterbodies and at the natural waterbody of Alligator Creek

Waterhole. In some cases several individuals even shared similar long-term activity areas (Figure 6.67, 6.69, 6.70 and 6.71). Overlapping activity areas in the Ivanhoe Plains Irrigation Area can be seen between animals #6 and 1.8 (Figure 6.67), animals #1.13, 4.11, 1, 1.14, 1.18, 2.13, 2 and 2.6 (Figure 6.68), animals #7, 12, 8, 11, 4.9, 15, 16, 2.1 and 4 (Figure 6.69). Overlapping activity areas in the Packsaddle Plains Irrigation Channel and Lake Kununurra Foreshore can be seen for animals #1.16, 17, 1.7, 1.15 and 2.8 (Figure 6.70). The activity areas of two individuals #4.6 and #3.18 overlapped in the Alligator Creek Waterhole (Figure 6.71).

The daily activity areas of adult *V. mertensi* also often overlapped. For example, individuals were often observed utilising the same basking site less than 5 m from each other. Radio-tagged adult *V. mertensi* were also regularly observed passing within 5 m of another adult *V. mertensi* during observation days.

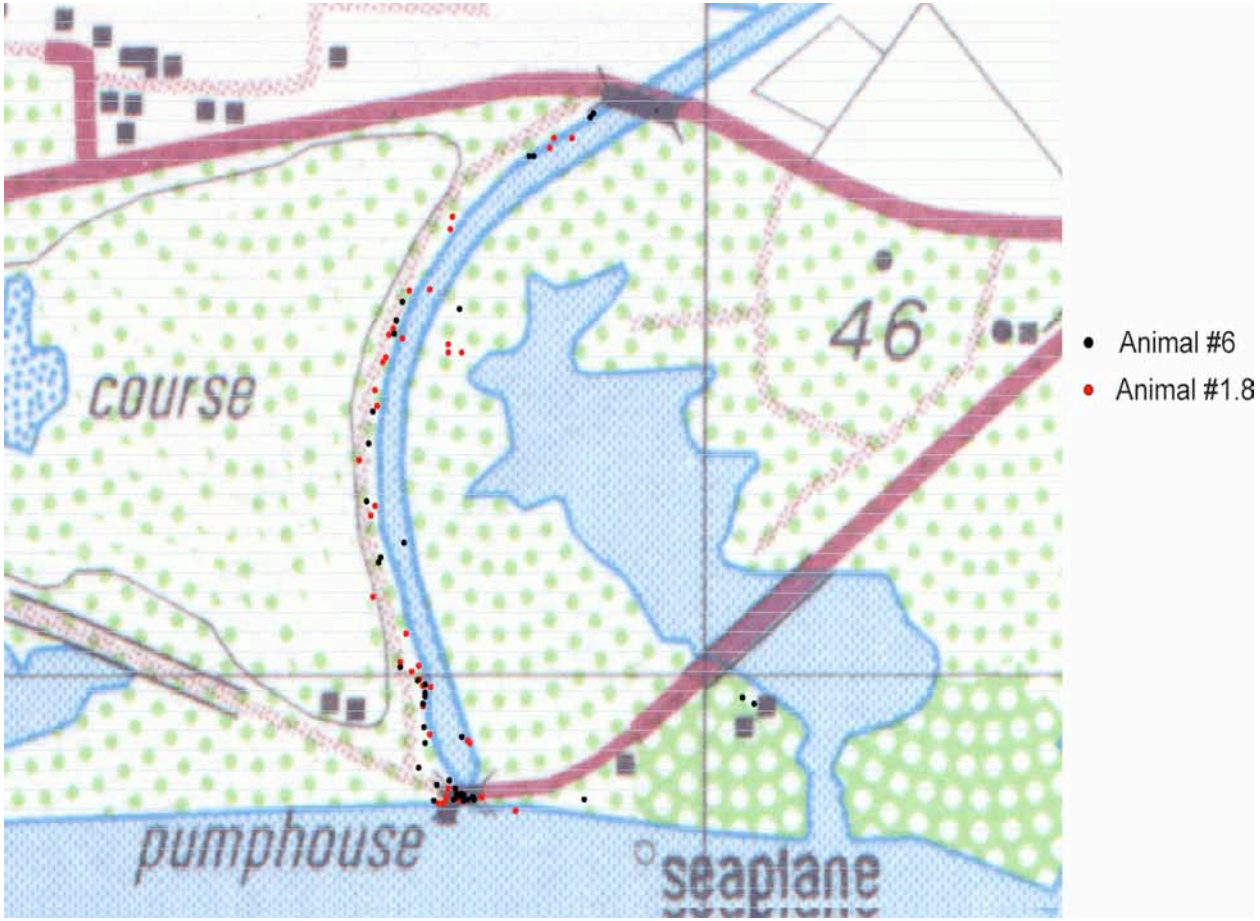


Figure 6.67: The overlapping long-term movements of two adult *V. mertensi* along the Main Irrigation Channel (IPM1) of the Ivanhoe Plains Irrigation Area between Lake Kununurra and a highway bridge. Positional fixes for animal #6 recorded between the 9/1/01 – 27/5/02 and animal# 1.8 recorded between 14/1/01 – 15/10/01.

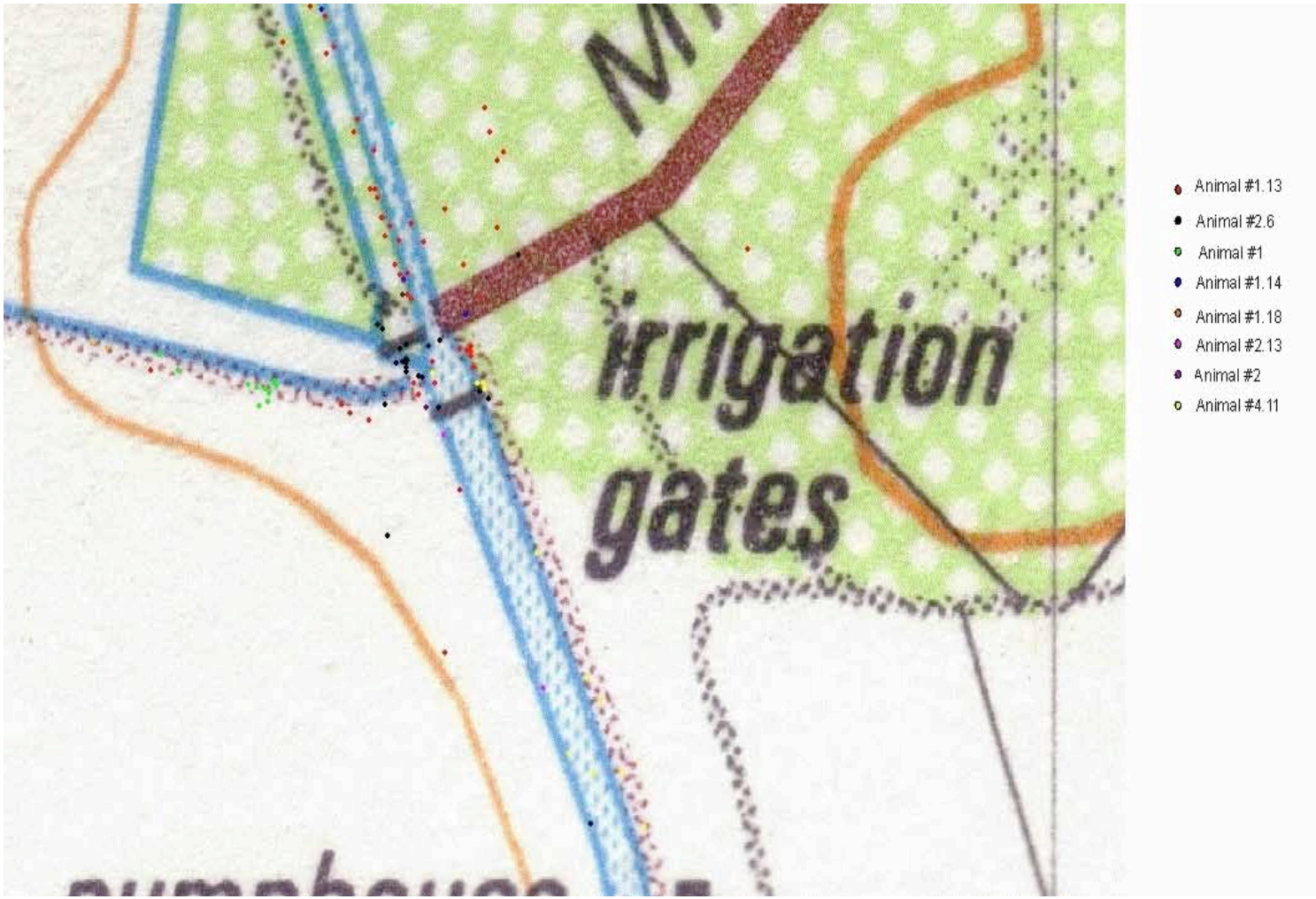


Figure 6.68: The overlapping long-term movements of eight adult *V. mertensi* in the Main Irrigation Channel (IPM1) and Supply Channel (S1) of the Ivanhoe Plains Irrigation Area. Positional fixes for animal #2.6 recorded between the 16/2/01 – 17/7/01, #1.13; 15/1/01 – 4/2/02, # 1; 12/1/01 – 12/2/02, # 1.14; 16/1/01 – 17/9/01, #2.13; 15/2/01 – 27/11/01, #2; 9/1/01 – 11/12/01 and #4.11; 28/7/01 – 27/5/02.

Figure 6.69: The overlapping long-term movements of nine adult *V. mertensi* in the Main Irrigation Channel of the Ivanhoe Plains Irrigation Area (IPM1), parallel Supply Channel (S2) and a swamp on the eastern side of IPM1. Positional fixes for animal #7 recorded between the 10/1/01 – 17/4/02, # 12; 11/1/01 – 22/3/02, #8; 10/1/01 – 10/7/02, #4; 9/1/01-29/1/02, #11; 11/1/01-15/5/02, #4.9; 24/7/02-24/2/02, #15; 12/1/01-5/6/01, #16; 12/1/01-5/6/01 and #2.1; 23/1/01-8/3/01.

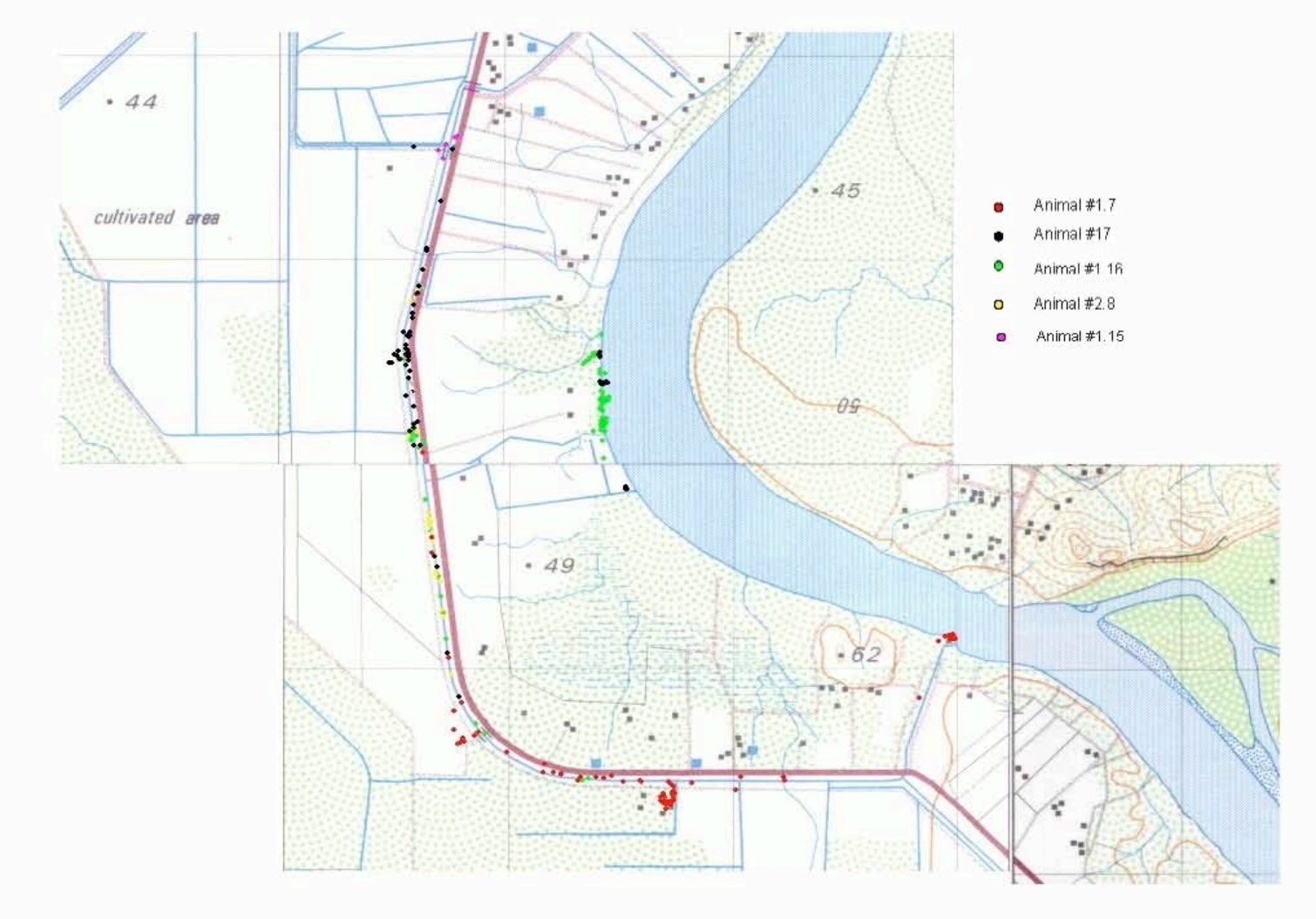


Figure 6.70: The overlapping long-term movements of five adult *V. mertensi* in the Packsaddle Plain Main Irrigation Channel (PSMIC) and Lake Kununurra Foreshore (LKF). Positional fixes for animal #1.7 recorded between the 12/1/01 – 12/1/03, #17; 12/1/01-23/1/03, #1.16; 17/1/01-28/1/03, #2.8; 20/1/01-20/9/01 and #1.15; 17/1/01-22/4/01.

Figure 6.71: The overlapping long-term movements of two adult *V. mertensi* in the Alligator Creek Waterhole (ACW). Positional fixes for animal #4.6 recorded between the 11/6/01 – 31/10/01 and animal# 3.18 recorded between 11/6/01 – 22/10/01.

6.5.17 Antagonism between *V. mertensi* individuals

On only one occasion was an antagonistic encounter between two adult *V. mertensi* observed during the field study. On this occasion two adults were observed engaged in a combat on the banks of the PSMIC as described below.

A radio-tagged adult, animal # 8 (sex = ♂, SVL = 500 mm) was observed in combat with an unknown adult *V. mertensi* on the 9/4/01. The encounter involved the two adults emerging from the water and beginning an upright 'arm-in-arm' clinching wrestle on a nearby channel access road (Plate 6.4). They were observed 'clinching' each other in an upright bipedal position for a period of approximately 30-60 seconds. Following this embrace they broke apart and promptly returned to the water separately.

Plate 6.4: Frame from a series of 5 photographs taken on the 9/4/01 depicting a combat between two adult *V. mertensi* (one a confirmed ♂) on a channel access road adjoining the PSMIC.

6.5.18 Interactions between *V. mertensi* and other species

During the field study two observations were made that indicated *V. mertensi* may be preyed upon by *C. johnstoni*. Anecdotal evidence of a further reptile predator was also collated. These are described below.

Observations

On two occasions *V. mertensi* were observed carrying injuries consistent with an attack by *C. johnstoni*. On the 10/1/01, an adult was captured in the IPM1 channel

with two teeth holes in its abdomen. The holes were located on the lower ventral surface of the abdomen approximately 1 cm apart. The holes were of dimensions 1.2 cm x 1.0 cm and 1.0 cm x 0.8 cm and were both approximately 0.5 cm deep (Plate 6.5). On a second occasion, during the late dry season of 2002, another adult was sighted in the field with its rear left hind limb severely lacerated. This injury was also consistent with an attack by *C. johnstoni*. The laceration was so severe that only bone remained and all skin and tissue was absent (Plate 6.6).

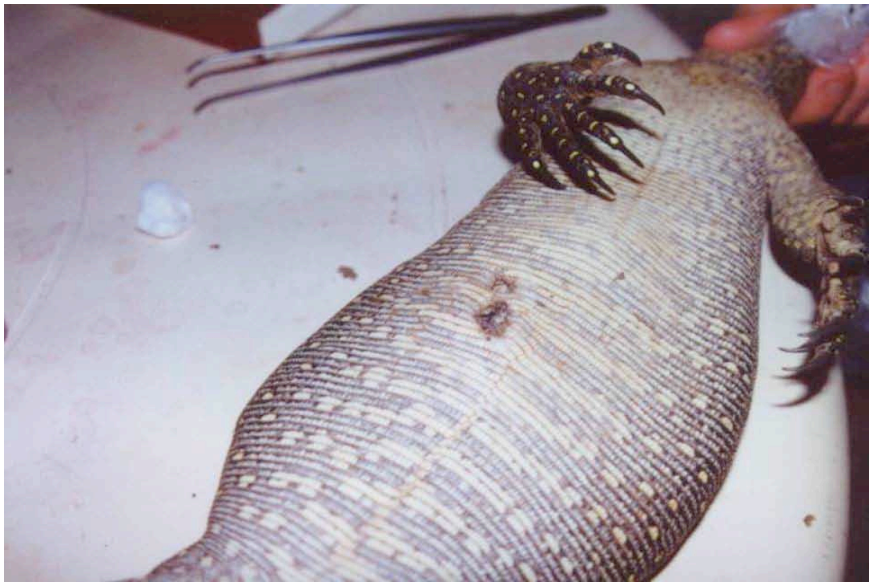


Plate 6.5: Two large teeth holes in the abdomen of an adult *V.mertensi*. The individual captured in the main irrigation channel (IPM1) of the Ivanhoe plains Irrigation Area on the 10/1/01.

Plate 6.6: A severe laceration on the left hind limb of an adult *V. mertensi*. Individual observed on the bank of the main irrigation channel (IPM1) of the Ivanhoe Plains Irrigation Area during the late dry season of 2002.

Anecdotal report

Location: Natural watercourse, Deception Range, 30 km southwest of Kununurra

I obtained a photograph and anecdotal evidence describing the consumption of a sub-adult *V. mertensi* tail-first by a water python (*Liasis fuscus*). The photo was taken at a natural waterhole known as Deception Range Waterhole approximately 30 km southwest of Kununurra (exact location unknown) during the early dry season. I was informed the photograph depicts the outline of a sub-adult *V. mertensi* inside the stomach of the water python (Plate 6.7). The photographer also described how he observed the water python consuming the sub-adult *V. mertensi* over the course of a day (pers. comm, John Mack).

Plate 6.7: The outline of sub-adult *V. mertensi* in the stomach of a water python (*Liasis fuscus*). Photograph taken at Deception Range Waterhole during the late dry season (Photograph John Mack).

6.5.19 Co-existence of *V. mertensi* and *C. johnstoni*

A total of 61 surveys of the Ivanhoe Plains Main Irrigation Channel (IPM1) were completed during the years 2001, 2002 and 2003 for *V. mertensi* and *C. johnstoni*. Twenty daylight surveys were completed between the 10/1/01 - 18/2/01. Twenty one surveys were completed between the 4/2/02 - 13/5/02. Of these 17 were completed during daylight hours and 4 were completed at night. Twenty surveys were completed between the 3/1/03 - 3/2/03. Of these 10 were completed during daylight hours and 10 were completed at night.

All surveys combined show the highest number of *C. johnstoni* were sighted between 0 - 8 km downstream of the M1 Pumphouse (Lake Kununurra) (Figure

6.72). Generally a higher number of *C. johnstoni* were sighted in the 1st 7 km's of IPM1 compared to *V. mertensi*. This was the case in all three survey years (Figure 6.72). In all three survey years few *C. johnstoni* were sighted between the 8th km of IPM1 and the end of the survey section at 12 km (Figure 6.72).

Varanus mertensi sightings were generally evenly spread along the 12 km length of IPM1. In 2001 and 2002 the greatest number of *V. mertensi* were in the 6th and 7th km of IPM1 (Figure 6.1). Sightings of *V. mertensi* and *C. johnstoni* showed the two species coexist in many sections of the 12 km length of IPM1 (Appendix 6.1). The highest number of *V. mertensi* sighted along the 12 km's of IPM1 was 14 individuals (Appendix 6.1, 2001 and 2003). This equates to a minimum population density of 1.17 individuals km^{-1}.

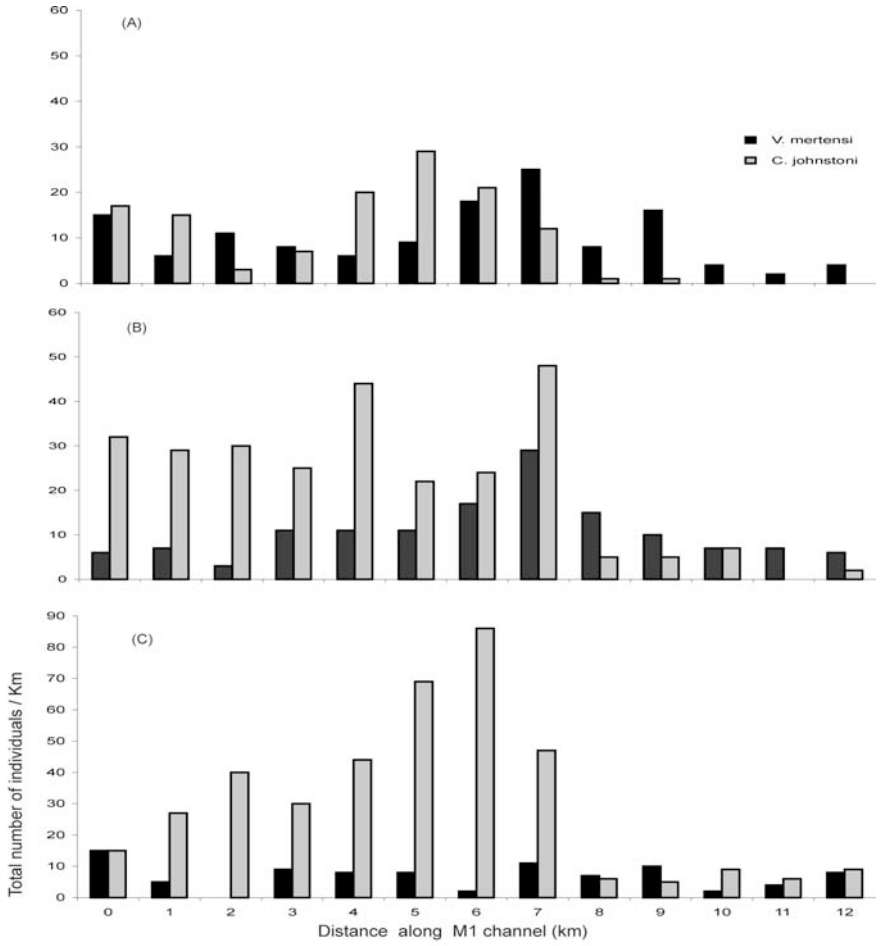


Figure 6.72: Sightings of *V. mertensi* and *C. johnstoni* recorded during 20 surveys completed between the 10/1/01 - 18/2/01 during daylight hours (A). (B) 21 surveys completed between the 4/2/02 - 13/5/02; 17 completed during daylight hours and 4 during the night. (C) 20 surveys completed between the 3/1/03 - 3/2/03; 10 completed during daylight hours and 10 during the night.

6.6 Discussion

6.6.1 Use of burrows

Varanus mertensi emerged from their overnight refuge burrows at around 08:00 hrs (WST). Individuals usually remained active throughout the day until retreating back into a burrow between 16:00 - 16:30 hrs (WST). However, when disturbed or threatened some individuals retreated to refuge burrows during their active day. It has been suggested (Auffenberg 1983; Traeholt 1995) that varanids use burrows both overnight and as a predator refuge when disturbed or threatened. Observed burrow use by *V. mertensi* in this study supports this suggestion.

Burrow selection by *V. mertensi* indicated that individuals were aware of burrow locations within their daily activity areas. *Varanus mertensi* rapidly travelled large distances, late in their active day, to return to a preferred overnight refuge burrow. Individuals were also observed promptly retreating into close by burrows when disturbed. These observations suggest individuals were not only aware of the location of their preferred overnight refuge burrows but also the location of burrows that could be utilised if disturbed or threatened. Traeholt (1995) and Tsellarius and Menshikov (1995) reported *V. salvator* and *V. griseus* repeatedly returned to the same preferred burrows within their activity areas. Spatial awareness of key locations within daily activity areas has also been reported for several other varanids including *V. glauerti* (Sweet 1998), *V. tristis* (Thompson *et al.* 1999) and *V. gouldii* (Thompson 1995).

Burrow entrances close to water level were not observed being used as basking sites by *V. mertensi*. Only one individual was observed basking at the entrance to a rock crevice burrow away from the waters edge. Generally individuals emerged from their soil bank burrows and moved to a preferred basking site nearby or alternatively immediately commenced aquatic activity. Traeholt (1995) reported *V. salvator* rarely use burrow entrances as basking sites and Auffenberg (1983; 1994) reported *V. bengalensis* utilising numerous basking sites away from their burrow entrances. This suggests the burrow entrances of these two varanids and *V. mertensi* do not represent preferred basking sites. Rather the burrow entrances of *V. mertensi* on the waters edge may reflect the convenience of locating burrows close to the water for a highly aquatic varanid (Christian and Weavers 1996; Cogger 1992; Mayes 2003, Shine 1986; Thompson *et al.* 2005). Numerous observations of

individuals promptly entering and retreating to burrows, from the water, illustrate the convenience of this burrow entrance location.

This study showed rock crevice burrows are also occasionally used by *V. mertensi*. This suggests some flexibility in the location and characteristics of their burrows. Similar variation has also been reported in the location and characteristics of burrows used by *V. bengalensis* (Auffenberg 1983; 1994), *V. komodoensis* (Auffenberg 1981), *V. griseus* (Tsellarius and Menshikov 1995) and *V. salvator* (Traeholt 1995).

6.6.2 Burrow characteristics

The majority of soil bank burrows used by *V. mertensi* consisted of a straight lumen with no branches and a single terminal chamber. Burrows only deviated around obstacles such as rocks. Similarly, soil burrows used by *V. bengalensis* consisted of a straight non-branched lumen except where obstacles were encountered during excavation (Auffenberg 1983). In contrast, burrows of *V. salvator* (Traeholt 1995), *V. komodoensis* (Auffenberg 1981) and *V. griseus* (Tsellarius and Menshikov 1995) were complex, consisting of many branches and multiple chambers with some side chambers possibly being used as egg chambers (Auffenberg 1981; Traeholt 1995; Tsellarius and Menshikov 1995). In contrast, female *V. bengalensis* (Auffenberg 1981), *V. varius* (Carter 1999), *V. rosenbergi* (Green *et al.* 1999) and *V. niloticus* (Cowles 1930) deposit their eggs in termitaria or especially excavated nest chambers rather than in their simple refuge burrows. It is not known where female *V. mertensi* deposit their eggs. However, the simple burrows of *V. mertensi* preclude the use of side chambers for egg deposition, as has been suggested for some other varanids (Auffenberg 1981; Traeholt 1995; Tsellarius and Menshikov 1995). This suggests female *V. mertensi* may excavate separate nests to deposit their eggs.

6.6.3 Basking sites

Varanus mertensi, like most varanids bask during their active day. Unlike terrestrial and arboreal varanids that use basking sites distributed throughout the terrestrial and arboreal environments (Auffenberg 1988; 1994; Auffenberg *et al.* 1991; Thompson 1993; 1994), the basking sites of *V. mertensi* are concentrated close to the water's edge. Basking sites close to the water are similar to those used by the semi-aquatic *V. salvator* and *V. niloticus*. For example, Gaulke (1999) described a

regular basking site used by *V. salvator* as a logged tree adjoining an open trail within a flooded palm-oil plantation and Cowles (1930) reported *V. niloticus* basking on driftwood, overhanging rocks and branches and on downpressed reeds on the edge of watercourses. Similarities in the basking sites used by these semi-aquatic varanids suggests the use of basking sites on the water's edge may be common amongst semi-aquatic varanids.

Basking sites close to the water's edge facilitate more time for aquatic activity such as foraging by semi-aquatic varanids. As discussed in Chapter 3, *V. mertensi* regularly emerge from the water to bask throughout their aquatically active day. If basking sites close to the water's edge are used then individuals can promptly resume their aquatic activity following periods of basking.

The physical characteristics of basking sites used by *V. mertensi* were similar to those reported for other varanids such as *V. bengalensis* (Auffenberg 1994; Auffenberg *et al.* 1991), *V. olivaceous* (Auffenberg 1988), *V. caudolineatus* (Thompson 1993) and *V. gouldii* (Thompson 1994). Sites are chosen to maximise heat gain in the shortest possible time. For example, sites used by *V. mertensi* were always in direct sunlight and on substrates that aided in conductive heat gain such as on cement or rock. *Varanus mertensi* choose basking sites based on their physical properties much like other varanids but select predominantly sites close to the water's edge.

6.6.4 Foraging areas

Varanus mertensi forage mainly in aquatic areas and through riparian vegetation bordering waterbodies. Individuals were also occasionally observed opportunistically foraging for tourist leftovers in caravan parks away from the water's edge (Chapter 4). This is similar to reports on the foraging areas of other semi-aquatic varanids such as *V. salvator* (Dryden and Wikramanayake 1991) and *V. niloticus* (Luiselli *et al.* 1999). For example, *V. salvator* has been reported opportunistically foraging for leftovers in tourist villages on islands of the Philippines (Traeholt 1994). *Varanus niloticus* has also been reported opportunistically foraging through villages bordering rivers in Natal (Cowles 1930).

Varanus mertensi often concentrated their foraging movements along the bank/water interface, an area abundant in an available prey resource, *Holthuisana* sp. crabs that reside in burrows in this zone (Chapter 4). Foraging in this area also allows

individuals to remain vigilant of both the water and nearby riparian vegetation simultaneously while foraging (Chapter 4). Area-concentrated foraging behaviour has also been reported for *V. niloticus*, that feed on crabs along the banks of marshes of central Africa (Luiselli *et al.* 1999) and other semi-aquatic varanids such as *V. salvator* (Gaulke 1991; Traeholt 1994; 1997a,b), *V. semiremex* (James *et al.* 1992) and *V. mitchelli* (James *et al.* 1992; Shine 1986) that also concentrate their foraging efforts on areas with high aquatic prey resources. This study showed *V. mertensi* like other semi-aquatic varanids, opportunistically utilises available aquatic prey resources through concentrating its foraging efforts.

6.6.5 Daily behaviour

After emerging from overnight refuge burrows *V. mertensi* spent considerably more of their active day swimming than walking. This shows *V. mertensi* swim predominantly through their daily activity areas unlike terrestrial varanids such as *V. gouldii* (Thompson 1994; 1995) and arboreal varanids such as *V. tristis* (Thompson *et al.* 1999). A greater time spent swimming presents more opportunities for *V. mertensi* to forage in the aquatic environment. This was found to be the case as individuals also spent far greater time foraging while swimming compared to walking. Foraging predominantly in the water has also been reported for other semi-aquatic varanids. For example, Gaulke (1999) reported *V. salvator* rarely left flooded palm oil plantations while numerous authors (Angelici and Luiselli 1999; Charlton 1973; Cowles 1930; Cloudsley-Thompson 1969; Edroma and Ssali 1983; Yeboah 1993) reported *V. niloticus* regularly swimming in streams and watercourses during its daily activity. It would be expected that extensive aquatic foraging should be reflected in a diet containing mostly prey of aquatic origin. This has been shown for both *V. salvator* and *V. niloticus* (Carl 1993; Cissé 1972; Cowles 1930; Edroma and Ssali 1983; Gaulke 1991; Luiselli *et al.* 1999; Traeholt 1994; 1997) and is also the case for *V. mertensi* (Chapter 4).

Six *V. mertensi* observed in both wet and dry seasons spent 37% of their active day basking. Basking during the day was shown to re-elevate T_b reduced through activity in cold water and assist in maintaining T_bs within a narrow preferred range (Chapter 3). Alternatively, activity in warm water, close to preferred T_b, negated the need to bask (Chapter 3). This use of water to behaviourally maintain

preferred T_bs was also reported for the aquatically active *V. salvator* (Wikramanayake 1995).

6.6.6 Daily movements

Distances moved during an active day by different *V. mertensi* found in different areas varied, much like other varanids. Variation in the distances moved by individuals observed on different days was also observed. This shows daily distances moved by *V. mertensi* vary among locations, individuals and days on which individuals were observed. Variation in daily distances moved by different individuals of the terrestrial *V. gouldii* (Thompson 1992) and arboreal *V. tristis* (Thompson *et al.* 1999) have also been reported.

The greatest daily distance moved along an irrigation channel by a *V. mertensi* was over 2.5 km. Other varanids have also been reported moving substantial distances during an active day. These include *V. varius* reported to move 1.63 km day^{-1} (Weavers 1993), *V. griseus* 0.1 – 2.5 km day^{-1}(Vernet *et al.* 1988), *V. komodoensis* 1.8 km day^{-1}(Auffenberg 1981) and *V. albigularis* 4 km day^{-1}(Alberts 1994). Other arboreal and saxicolous species have been reported moving smaller daily distances. For example, a mean on ground distance of 139 m for *V. tristis* (Thompson *et al.* 1999), between 16-81 m for *V. glauerti* (Sweet 1999), 14 – 156 m for *V. caudolineatus* (Thompson 1993) and 53 – 116 m for the saxicolous *V. glebopalma* (Sweet 1999). The semi-aquatic *V. salvator* was reported to move 252 – 470 m day^{-1} (Gaulke *et al.* 1999).

Another Australian varanid, the terrestrial *V. gouldii*, was reported to move a point-to-point distance of 980 m day^{-1} in an urban cemetery (Thompson 1992). Thompson (1992) suggested these values may be underestimates since numerous cotton spools, used to measure movement distances, broke during deployment. It is thus probable that the daily distances moved by *V. mertensi* and *V. gouldii* regularly exceed 1 km. This suggests these two closely related species use their daily activity areas in a similar way.

The daily activity areas of *V. mertensi* of between 0.1 – 1 ha are similar to those reported for *V. rosenbergi* of between 0.1-1.4 ha (Green and King 1978) and foraging areas of *V. gouldii* in an urban cemetery of between 0.31 – 0.56 ha (Thompson 1992).

The daily speed of movement of *V. mertensi* was similar to that reported for *V. gouldii.* The daily speed of movement of six *V. mertensi* ranged between 0.2 – 2.55 m min^{-1} with a mean speed of 1.4 m min^{-1}. The daily speeds of two *V. gouldii* were 1.59 m min^{-1} and 2.78 m min^{-1} (Thompson 1995). Thompson (1995) also observed *V. gouldii* moving rapidly between foraging areas at speeds up to 27.6 m min^{-1}. *Varanus mertensi* were also observed rapidly swimming between aquatic foraging areas at speeds up to 14 m min^{-1}. This shows both varanids move throughout their daily activity areas at similar speeds. This combined with comparable daily movement distances and size of activity areas shows *V. mertensi* move in an analogous way to the closely related *V. gouldii*. The only difference in the daily movements of the two taxa being that *V. mertensi* concentrate their daily movements to in and around water unlike *V. gouldii* which move through terrestrial areas.

6.6.7 Long-term activity areas

Varanus mertensi found in irrigation waterbodies, much like other wide ranging varanids, moved over large areas of up to 31.8 ha. For example, other wide ranging varanids have been reported to move over comparable sized areas including; *V. rosenbergi*: 1.7 – 43 ha (Green and King 1978), *V. tristis*: 3.7 – 40.3 ha (Thompson *et al.* 1999), *V. bengalensis*: 4 – 33 ha (Auffenberg *et al.* 1991), *V. albigularis*: 6.1 – 18.3 ha (Phillips 1995), *V. giganteus*: 2.9 – 21.5 ha (King *et al.* 1989), *V. salvator*: 1.7 -22.6 ha (Gaulke *et al.* 1999), *V. varius*: 65 ha (Weavers 1993), *V. komodoensis*: 4200 ha (Auffenberg 1981) and *V. griseus*: 31.9 – 98.4 ha (Stanner and Mendelssohn 1987). However, *V. mertensi* found in natural waterbodies were only observed moving over areas of up to 0.5 ha. This may be an artifact of the loss of many radio-tagged individuals at natural waterbodies which suggests individuals moved to unknown locations. The unknown movements of such individuals may be as wide ranging as in irrigation areas. In this area the results of this study are inconclusive.

The activity areas of *V. mertensi*, much like other semi-aquatic varanids such as *V. salvator* (Auliya and Erdelen 1999; Pandav and Choudhury 1996; Traeholt 1997) and *V. niloticus* (Angelici and Luiselli 1999) were concentrated around water. This was reflected in the shape of activity areas which resembled the shape of waterbodies in which individuals were found. It is possible that *V. mertensi*

occasionally move between spatially separated waterbodies through the terrestrial environment. However, extended periods of terrestrial activity were not supported by the findings of this study.

6.6.8 Activity area and body size

The activity areas of reptiles have been shown to be positively correlated with body size (Christian and Waldschmidt 1984; Lewis and Saliva 1987; Rose 1982; Turner *et al.* 1969). However, considering reptiles with similar foraging modes and within narrow size ranges often reveals no effect of body size on activity area (Christian and Waldschmidt 1984). Several studies of varanids including *V. glauerti* and *V. glebopalma* (Sweet 1999), *V. gouldii* (Thompson 1994) and *V. komodoensis* (Auffenberg 1981) have shown activity areas to be positively correlated with body size. This study found no significant effect of body size (body mass or SVL) on the activity area of *V. mertensi*. This may reflect the narrow range of different size adult *V. mertensi* examined in this study. Alternatively, as has been suggested by others (Christian and Waldschmidt 1984; Rose 1982), other factors such as habitat productivity, social factors, population density and seasonal climatic changes may override and mask the effects of body size on determining activity area.

Generally the activity areas of different sized *V. mertensi* were close to the size of areas predicted for an individual based on its body size (snout-vent length) (see Figure 6.73 and Table 6.74 for references). The activity areas of 19 out of 31 (61.3%) *V. mertensi* fell within the 95% confidence limits describing the effect of SVL on activity area size (Figure 6.73, Table 6.74). Of the 12 *V. mertensi* that fell outside these limits, two were female, three were males and seven were of unknown sex (Figure 6.73). This illustrates the similar size of the predominantly linear activity areas of the medium-sized *V. mertensi* and other medium-sized varanids of similar body size such as *V. gouldii* (Figure 6.73; Table 6.74).

Table 6.74: The activity areas of four varanid species for which body mass and snout-vent length of individuals was reported. All activity area estimates made through direct measurement. The activity areas of males and females, body mass, snout-vent length, number of positional fixes and the duration over which they recorded also shown. – denotes data not available and * data recorded during the mating season.

Species	Body mass (grams)	SVL (mm)	No. of fixes	Duration (months)	Activity area (ha)	Source
V. rosenbergii	990	-	17	24	4.14	(Green and King 1978)
	1320	-	13	74	16.19	
	1465	-	15	46	43.70	
	700	-	10	32	3.36	
V. gouldii (male) *	464	330	69	2	6.5	(Thompson 1994)
	740	340	34	1	32.09	
	468	330	62	2	3.36	
	710	345	62	2	33.40	
V. gouldii (female)*	300	334	39	1	2.18	
	330	300	75	2	1.6	
	280	290	56	1	2.23	
	393	310	74	2	2.02	
	465	335	37	1	2.43	
	448	315	72	2	3.28	
V. glebopalma (male)	280	304	209	-	7.76	(Sweet 1999)
	265	301	247	-	7.45	
	114	232	204	-	3.67	
V. glebopalma (female)	133	248	248	-	3.97	
	125	243	243	-	3.5	
	133	251	251	-	4.56	
	118	237	237	-	6.7	
V. glauerti (male)	92	213	134	-	1.32	(Sweet 1999)
	141	246	113	-	7.36	
	99	216	46	-	2.41	
	75	201	62	-	1.25	
	64	188	32	-	0.73	
V. glauerti (female)	83	216	111	-	1.25	
V. salvator	400	275	26	1	4.9	(Gaulke *et al.* 1999)
	1000	375	16	< 1	13.7	
	1200	425	23	< 1	22.6	
	770	355	20	< 1	5.3	
	7200	710	14	< 1	1.5	
	3500	545	10	< 1	1.7	

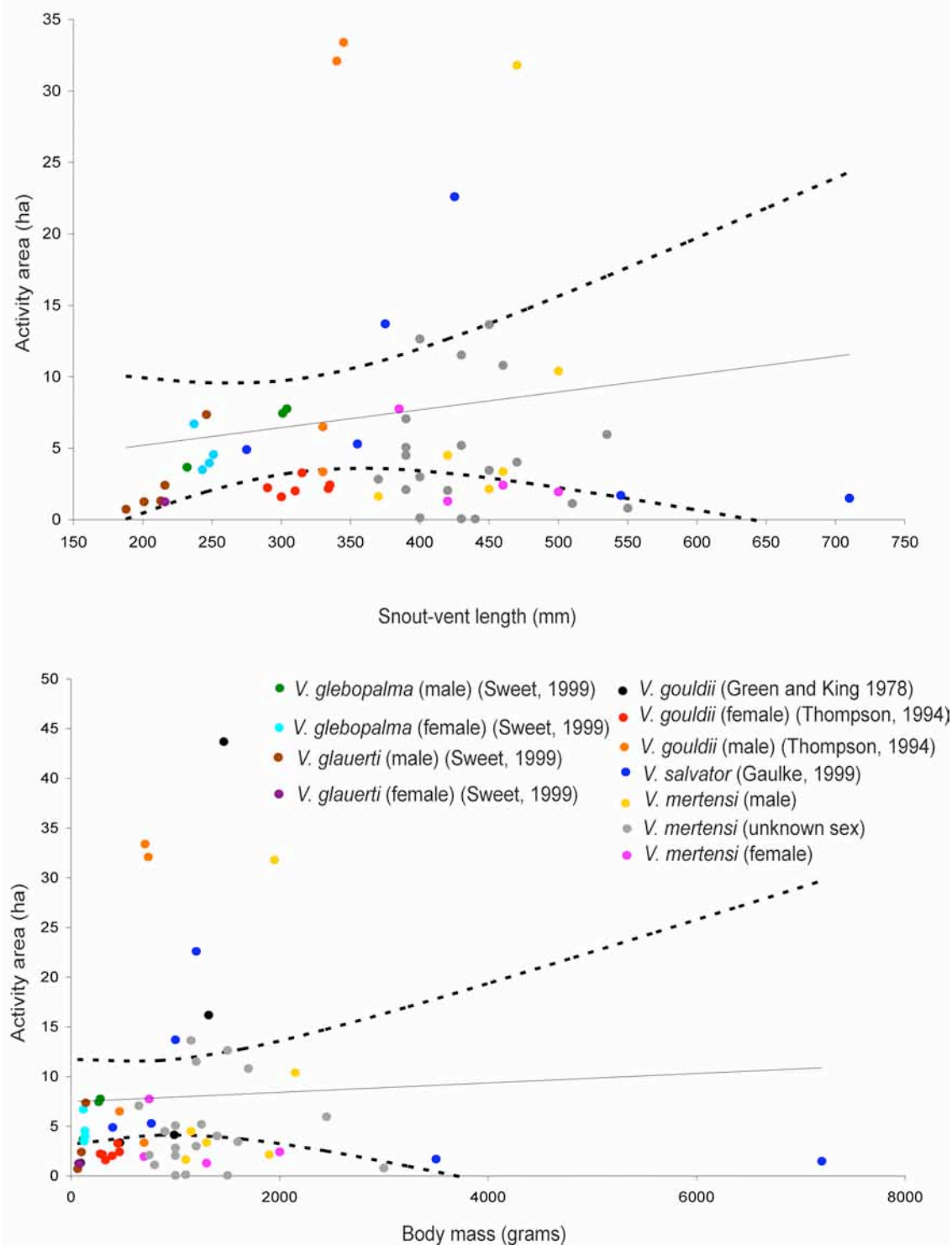


Figure 6.73: The relationship between both body mass (top) and snout-vent length (bottom) and activity area for five varanids including the semi-aquatic *V. mertensi* and *V. salvator*. Additional data taken from available literature and 95 % confidence limits exclude *V. mertensi*.

6.6.9 Core activity areas

Many varanids utilise core activity areas within their long-term activity areas, including *V. rosenbergi* (Green and King 1978), *V. gouldii* (Thompson 1995), *V. caudolineatus* (Thompson 1993), *V. glebopalma* (Sweet 1999), *V. glauerti* (Sweet 1999), *V. bengalensis* (Auffenberg *et al.* 1991) and *V. salvator* (Gaulke *et al.* 1999). Likewise, *V. mertensi* were found to use core activity areas within their long-term activity areas. Additionally, several individuals moved seasonally between the same core activity areas in consecutive years suggesting this may be a general pattern of behaviour. It has been suggested that varanids forage throughout core activity areas until such time as prey resources fall below levels warranting further foraging effort. Individuals then move in search of more prosperous areas in which to forage (Thompson 1995). Although such moves are not without risk the benefits of encountering more favourable prey resources may outweigh the cost of remaining in a core area with depleted prey resources. The movement of several *V. mertensi* from irrigation channels to the Lake Kununurra Foreshore during dry season months, when the dominant prey of *V. mertensi*, *Holthuisana* sp. crabs maybe less obtainable in irrigation channels, supports this suggestion (Chapter 4). This finding also suggests individuals may retain knowledge of areas with seasonally favourable prey resources based on prior experience and move to these areas at such times.

6.6.10 Mating period movements of males

Male varanids move more extensively in search of reproductively receptive females during mating months (*V. gouldii*, Green and King 1978; Thompson 1994; *V. bengalensis*, Auffenberg *et al.* 1991; *V. tristis*, Thompson *et al.* 1999; *V. albigularis*, Phillips 1995; and *V. glauerti*, Sweet 1999). Male *V. mertensi* also moved more extensively during the mating months of December – February. Two males moved out of their known activity areas during these months and could not be found despite widespread intensive search efforts, suggesting they may have moved a substantial distance in search of receptive females.

6.6.11 Seasonal Inactivity

Studies identifying inactivity by temperate and arid-zone varanids such as *V. rosenbergi* (Green and King 1978), *V. gouldii* and *V. panoptes* (Christian *et al*. 1995;

Christian and Weavers 1996), *V. varius* (Bustard 1968), *V. brevicauda* (Pianka 1970), *V. tristis* (Pianka 1971), *V. giganteus* (Stirling 1912), *V. griseus* (Absamatov 1976; Auffenberg *et al.* 1990; Stanner and Mendelssohn 1991), *V. caudolineatus* (Pianka 1969) and *V. niloticus* (Cowles 1930) have suggested a link with seasonally low temperatures. However, for *V. mertensi* many individuals became inactive during the dry season while others remained active, suggesting no such obligatory link (Chapter 3). Additionally, no link between a lack of water and seasonal inactivity was found for *V. mertensi*. This suggests dry season inactivity in some *V. mertensi* may be linked with a seasonal reduction in obtainable local prey resources. It is possible that the amount of prey obtainable by individual's falls below a threshold at which the energy expended in searching for prey outweighs the energetic benefit gained upon its capture. This is supported by data showing that the predominant prey of *V. mertensi*, *Holthuisana* sp, were less obtainable during the dry season (Chapter 4). Likewise, a link between seasonally low prey availability and inactivity has been suggested for other tropical varanids such as *V. glebopalma* (Sweet 1998), *V. scalaris* (Christian *et al.* 1999), *V. panoptes* (Christian *et al.* 1995) and *V. bengalensis* (Auffenberg *et al.* 1991) and receives further support in this study.

6.6.12 Lack of territoriality

No defense of defined territories amongst individual varanids is widely reported in wide-ranging active-foraging species (Auffenberg 1981; Auffenberg *et al.* 1991; Green and King 1978; Stanner and Mendelssohn 1987; Thompson 1992; 1994). The overlapping activity areas and daily movements of *V. mertensi* suggests that individuals similarly do not defend defined territories and exclude other individuals.

6.6.13 Combat between individuals

Combat between individuals has been widely reported in varanids (Auffenberg 1981; Carpenter *et al.* 1976; Davis *et al.* 1986; Deraniyagala 1958; Horn *et al.* 1994; Johnson 1976; Mccoid and Hensley 1991; Murphy and Mitchell 1974); Thompson *et al.* 1992; Tsellarius and Tsellarius 1997; Twigg 1988). Combat between *V. mertensi* individuals has also been reported in captivity (Horn *et al.* 1994; Greer 1989) and this study documents that combat occurs in the field. This

behaviour, however, was not common in the field, as indicated by the duration of the field study and only the one occasion on which combat behaviour was observed.

Several hypotheses have been proposed to explain combat in varanids including maintenance of social hierarchies (Daltry 1991) and access to reproductively receptive females by males (Mccoid and Hensley 1991). Horn *et al.* (1994) reported that combat between three captive male *V. mertensi* occurred either in the presence or the absence of a female suggesting access to reproductively receptive females was not underlying combat behaviour. The field combat sequence observed in this study occurred outside mating months and did not occur in the presence of individuals other than the two combatants (one male and an individual of unknown sex). This further suggests combat amongst *V. mertensi* is not underpinned by access to reproductively receptive females.

Interspecific differences in the combat behaviour of varanids have been shown to have a phylogenetic background (Horn *et al.* 1994). Horn *et al.* (1994) showed that Odatria species do not have a "clinch phase", whereby combatants wrestle "arm-in-arm" but other species have a distinct "clinch phase" during combat. In support of this, numerous authors have reported this clinch phase in non-Odatrian varanids (Auffenberg 1981; Thompson *et al.* 1992; Twigg 1988). The combat sequence observed between *V. mertensi*, a non-Odatrian species, in this study was similar to that described by (Horn *et al.* 1994) for three captive *V. mertensi* and included a "clinch phase".

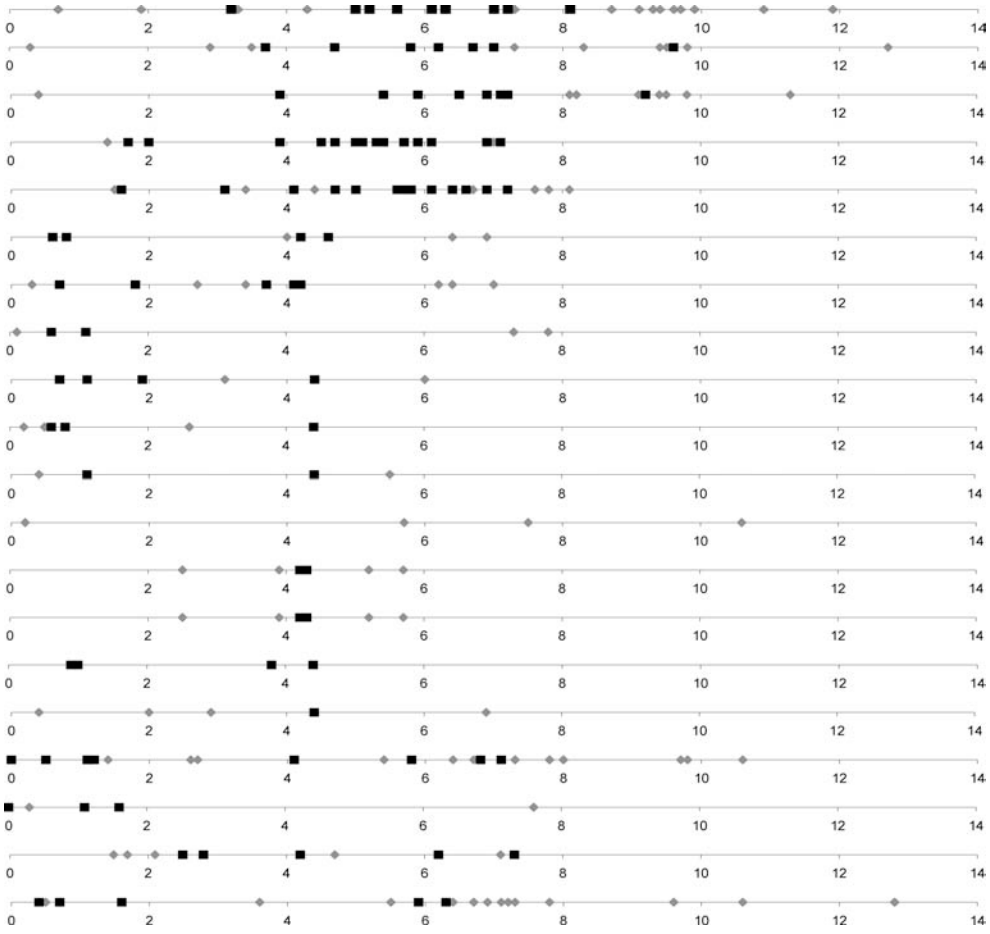
6.6.14 Interactions between *V. mertensi* and other reptiles

Few studies have identified natural predators of varanids (Browne-Cooper 1998; Christian 1995; Webb *et al.* 1982) other than humans (Abel 1998; Anon 1983; Das 1989; Inskipp 1984; Riquier 1998; Shine *et al.* 1996; Shine *et al.* 1998). Varanids are often accordingly considered a 'top predator' with few predators in their respective environments. Observational and anecdotal evidence compiled during this study suggests *V. mertensi* have at least two reptile predators, water pythons *L. fuscus* and freshwater crocodiles *C. johnstoni*. Evidence suggesting *C. johnstoni* prey upon *V. mertensi* in areas of the ORIS supports a report by Webb *et al.* (1982) who found *V. mertensi* in the diet of *C. johnstoni*. Predation on *V. mertensi* by *L. fuscus* is consistent with a report of a pygmy python, *Antaresia perthensis*, preying upon a *V. acanthurus* (Browne-Cooper 1998). The findings of this study

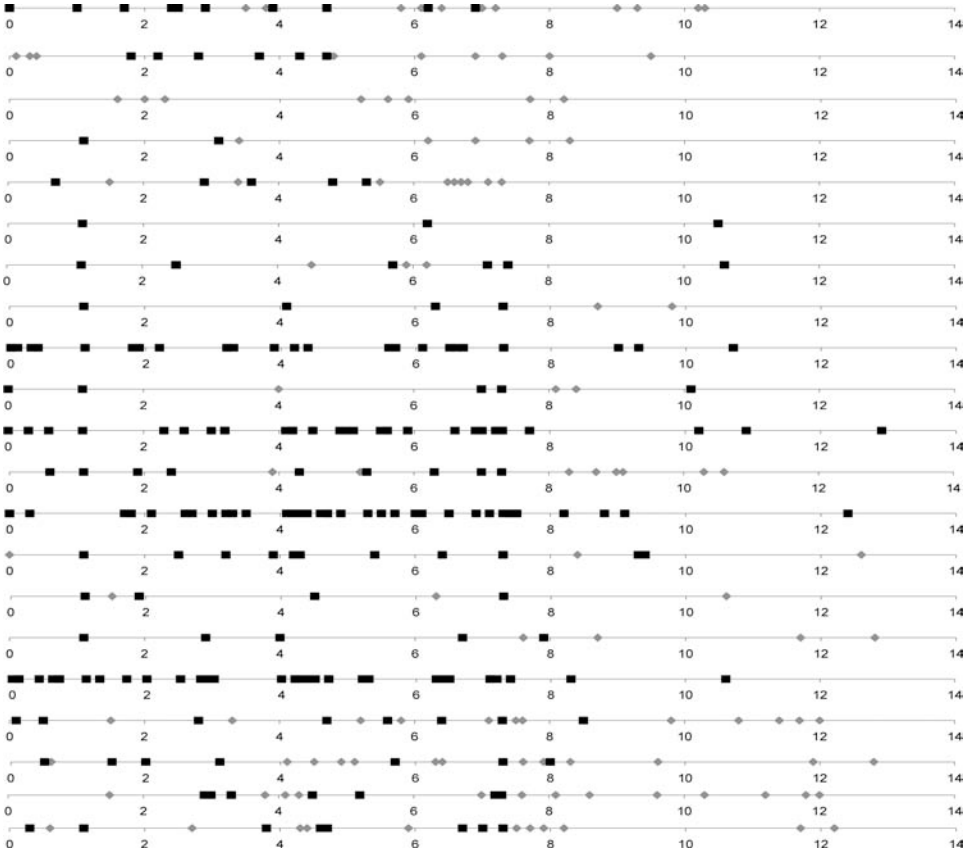
suggest *V. mertensi* is preyed upon by at least two other reptile species and maybe others. This being the case, *V. mertensi* should also be considered as a 'top predator' that preys upon many other species but also has several predators.

Varanus mertensi coexists with one of its predators, *C. johnstoni*. It might be anticipated that *V. mertensi*, owing to a risk of predation, would avoid *C. johnstoni*. However, no evidence of spatial partitioning between the species was found. Interestingly, the presence of eggs, possibly those of *C. johnstoni* in two stomachs and three scats of *V. mertensi*, also suggests *V. mertensi* prey on *C. johnstoni* (Chapter 4). Similar predation on eggs in the nests of *C. porusus* by *V. salvator* (Whitaker and Whitaker 1978) and by *V. panoptes* (Christian 1995) has also been reported. If *V. mertensi* utilise *C. johnstoni* eggs as a prey resource, then benefits gained by preying on eggs may outweigh the risk of predation by adult *C. johnstoni*. This may explain why *V. mertensi* do not avoid areas inhabited by *C. johnstoni*.

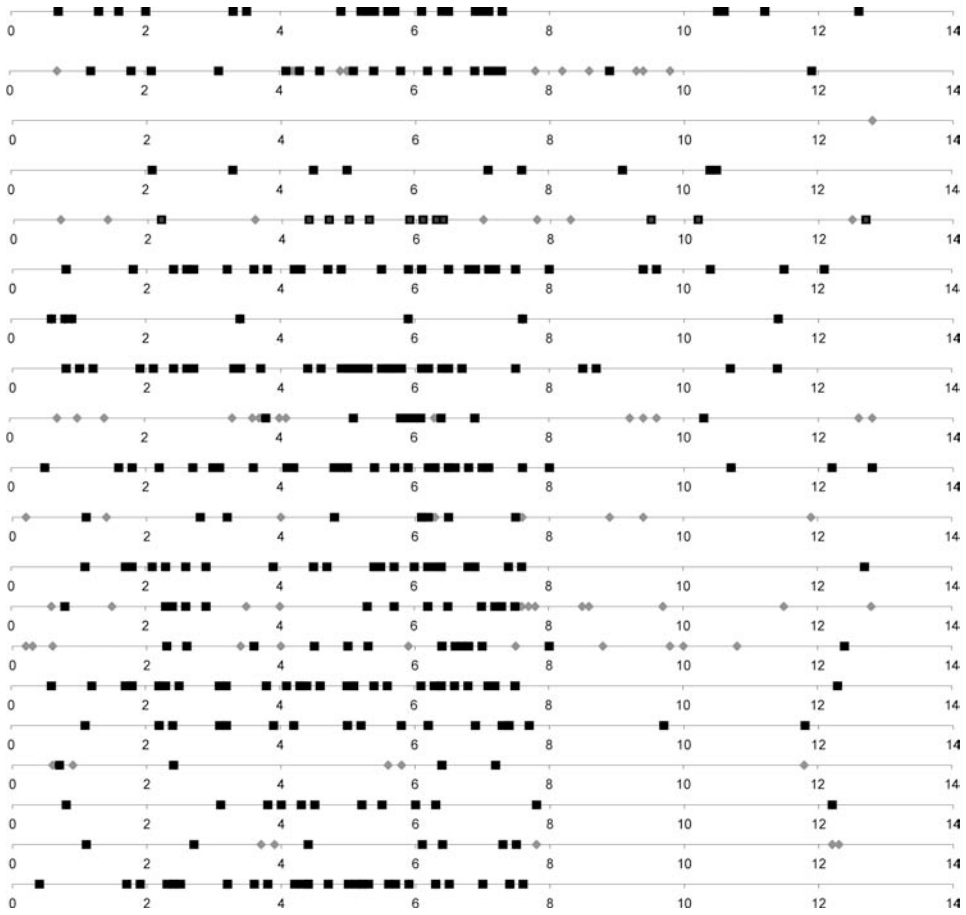
Appendix 6.1: Location of sighted *V. mertensi* ♦ and *C. johnstoni* ■ along the Main Irrigation Channel of Ivanhoe Plains Irrigation Area (M1) during all surveys in 2001, 2002 and 2003.
2001



2002



2003



-Chapter 7-

General discussion

7.1 Overview

The overall aim of this study was to examine the ecology and behaviour of *V. mertensi* found in waterbodies of the Ord River Irrigation Scheme (ORIS) and surrounding East Kimberley/Victoria River Downs bioregion of Western Australia. This provided some of the first insights into the life of a semi-aquatic faunal species in the ORIS. It also facilitated comparison between *V. mertensi* and other varanids expanding our knowledge of the family Varanidae.

Four aspects of the ecology and behaviour of *V. mertensi* were examined, including daily behaviour, diet and foraging behaviour, reproductive seasonality and spatial movements. Similarities and differences between *V. mertensi* and other varanids were discussed in each of four data chapters dealing with each of these aspects of the ecology and behaviour of *V. mertensi*. The first objective of this discussion is to integrate findings of each of these chapters to formulate a picture of the ecology and behaviour of *V. mertensi* compared to other varanids. The second objective of this chapter is to provide new insights into the life of *V. mertensi* found in waterbodies of the ORIS. This chapter will conclude by outlining scope for future studies of both *V. mertensi* and other fauna species found in the ORIS.

7.2 *Varanus mertensi*

7.2.1 Daily behaviour

Like many varanids, the diurnal *V. mertensi* retreats to overnight refuge burrows. Individuals also seek refuge in burrows when disturbed or threatened during their daily activity. This predator escape response has also been reported for other varanids (Auffenberg 1983; 1994; Traeholt 1995; Tsellarius and Menshikov 1995). The characteristics of burrows used by *V. mertensi* are generally similar to those reported for other varanids. However, one difference between the burrows of terrestrial varanids and those of the semi-aquatic *V. mertensi* and *V. salvator* (Traeholt 1995) is that burrow entrances are often located near water level in the banks of watercourses. This both aids in the aquatic lifestyle of *V. mertensi*, allowing

ease of access to the water upon emergence, and may be important in predator avoidance allowing prompt retreat from the water when disturbed.

Varanus mertensi emerge from and retreat to overnight refuge burrows at similar times to other varanids. After emerging from burrows, most varanids undergo a morning period of heat gain before maintaining relatively constant T_bs throughout their active day until T_b begins to fall just prior to retreat. This general daily temperature pattern was also observed in active *V. mertensi*. Like other semi-aquatic varanids, the daily behaviour of *V. mertensi* includes extensive aquatic activity. Activity in water rapidly changes the T_b of *V. mertensi* to the temperature of the water. As for other Australian varanids, the daily T_bs of active *V. mertensi* vary seasonally. Daily T_bs are lower during the dry season when water temperature is low compared to the wet season when water temperature is higher. Activity in cold water during the dry season is reflected in the daily behaviour of *V. mertensi* which includes more basking than in the wet season. Similar seasonal differences in daily behaviour have also been reported for other Australian varanids (Christian and Weavers 1996; Christian and Bedford 1996; King 1980). During the dry season *V. mertensi* need to regularly emerge from the water to bask and regain lost T_b. Alternatively, activity in warm water during the wet season allows extended periods of aquatic activity. To further facilitate aquatic activity, *V. mertensi* like other semi-aquatic varanids utilize basking sites on the water's edge. Such sites allow prompt return to the water following periods of basking.

Varanus mertensi is an active forager, like most varanids, with the exception of several ambush predators; *V. komodoensis* (Auffenberg 1978; 1981), *V. bengalensis* (Auffenberg 1983) and *V. glebopalma* (Sweet 1998). The movements of *V. mertensi* during their active day are wide-ranging much like other active foraging varanids. *Varanus mertensi* moves through its daily activity areas at speeds comparable to the similar-sized actively-foraging terrestrial *V. gouldii* (Thompson 1992). In contrast to terrestrial varanids but like other semi-aquatic varanids, *V. mertensi* forages in mainly aquatic areas including the water and through riparian vegetation close to the water's edge. This is reflected in the shape of the daily activity areas that closely resemble the shape of waterbodies.

Varanus mertensi draw on previous prey capture experience to maximise their foraging efficiency, concentrating their daily foraging efforts on areas with high prey resources. This ability has similarly been reported amongst other varanids

(Kaufman and Phillips 1992; Kaufman *et al.* 1994; Pianka *et al.* 2004; Thompson 1992; 1995; Traeholt 1993; Tsellarius *et al.* 1997). *Varanus mertensi* is also an opportunist adjusting its foraging behaviour to utilise available prey resources. This ability has been widely reported for other active foraging varanids (Christian 1995; Cisseé 1972; Gaulke 1991; James *et al.* 1992; Kaufman *et al.* 1994; Kennerson 1980; King and Green 1979; King *et al.* 1983; King *et al.* 1989; Losos and Greene 1988; McCoid and Witteman 1993; Secor and Phillips 1997; Stanner and Mendelssohn 1986; Thompson 1996; Traeholt 1994a,b; Tsellarius *et al.* 1997; Weavers 1989). Opportunism is reflected in the catholic diet of *V. mertensi*, which includes many different prey groups of aquatic origin. *Varanus mertensi* can successfully search for prey underwater an ability which aids substantially in the capture of aquatic prey. Other anatomical features that aid in the capture of aquatic prey include a dorsally compressed tail (Bedford and Christian 1996; Cogger 1992), which assists in swimming, and dorsally located external nares (Cogger 1992), which allow individuals to breathe while swimming on the surface.

7.2.2 Long-term behaviour

The large activity areas of *V. mertensi* are similar to those of other comparable-sized, wide-ranging varanids, but like other semi-aquatic varanids are concentrated around aquatic areas. This was reflected in long-term activity areas resembling the shape of waterbodies in which individuals were found. Like many other varanids, *V. mertensi* regularly move between core activity areas. As has been suggested for other varanids, movement between core activity areas by *V. mertensi* most likely reflects prey resource availability. Like other varanids, *V. mertensi*, only appear to remain in an area while aquatic prey resources are available and will move in search of new areas with available prey resources if they diminish.

Males of many varanid species move greater distances in search of reproductively receptive females during the mating season (Auffenberg 1981; 1988; 1994; Sweet 1999; Stanner and Mendelssohn 1987; Thompson 1994; Thompson *et al.* 1999). Male *V. mertensi* also moved more extensively during the mating season, suggesting they also actively search for reproductively receptive females.

Some *V. mertensi*, like other varanids, underwent periods of inactivity during their yearly activity pattern. Unlike temperate zone varanids that have been shown to become inactive due to seasonally low temperatures (Christian and Weavers 1994;

1996; King 1980) many *V. mertensi* remain active during the dry season while others become inactive. Absence of a link between water availability and inactivity further suggests dry season inactivity by some *V. mertensi* may be linked with low prey availability. One such prey resource which is less available during the dry season is the predominant prey item of *V. mertensi*, freshwater crabs (*Holthuisana* sp.). A similar link between low dry season prey resources and dry season inactivity by tropical Australian varanids such as the terrestrial *V. gouldii* and *V. panoptes* (Christian *et al.* 1995) and saxicolous *V. glebopalma* (Sweet 1999) suggests a common yearly activity pattern for these tropical Australian varanids.

Female *V. mertensi*, like other varanids, display synchronous breeding tactics, undergoing vitellogenesis during the mating season much like many other varanids. In contrast, male *V. mertensi* are asynchronous, undergoing pre-emptive spermatogenesis prior to the mating season. This male breeding tactic is similar to at least one other terrestrial varanid, *V. griseus*, that becomes seasonally inactive. This suggests an asynchronous breeding tactic may be common amongst male varanids that undergo inactivity. However, this is yet to be determined as few studies have examined the breeding tactics of male varanids that have been shown to become seasonally inactive.

Tropical Australian varanids vary in their reproductive seasonality with some species being dry season egg layers (King 1993; James *et al.* 1992; Pengilley 1981; Shine 1986; Sweet 1999) and others wet season egg layers (James *et al.* 1992; Shine 1986). Like some other tropical Australian varanids, *V. mertensi* fits into the category of a dry season egg layer. The timing of hatchling emergence is in part controlled by the onset of vitellogenesis in females, as males undergo pre-emptive spermatogenesis. Late wet season vitellogenesis enables females to build body condition during the wet season when prey resources such as freshwater crabs are readily available. Prey resource availability has been suggested as underlying the reproductive seasonality of other tropical varanid species and may also be the case for *V. mertensi*. Hatchling emergence is not only controlled by the deposition date of eggs following vitellogenesis but also incubation time before hatching. Early dry season egg deposition by *V. mertensi* and an incubation time of 9-10 months (Eidenmüller and Wicker 195l; Eidenmüller 1996) culminates in hatchlings emerging during the following wet season when prey resources available to them may also be high. This has also been suggested as underlying the reproductive seasonality of

tropical varanids (James *et al.* 1992; Wikramanayake and Dryden 1988) and may also be the case for *V. mertensi*. Overall, the reproductive seasonality of *V. mertensi* appears to give hatchlings a maximum chance of survival which would be anticipated given selection pressure acting on reproductive fitness.

7.2.3 Summary

The ecology and behaviour of *V. mertensi* is similar to that of most other similar-sized varanids only focused around aquatic areas. Its daily behaviour incorporates extensive aquatic activity and catholic diet includes numerous prey groups of aquatic origin. Foraging behaviour is wide ranging within the water and riparian vegetation on the water's edge. Individuals draw on previous prey capture experience to optimise their foraging efficiency and are capable of modifying their foraging behaviour to opportunistically utilise available aquatic prey resources. Movements between core activity areas may reflect changes in the availability of aquatic prey resources. Seasonal inactivity may also be linked with seasonally low aquatic prey resources. Reproductive seasonality focused around late wet season mating and early dry season egg deposition is similar to numerous other 'dry season egg-laying' tropical Australian varanids. Timing of vitellogenesis and egg deposition in females may also reflect seasonal availability of aquatic prey resources.

Varanus mertensi occupy a similar ecological niche to other semi-aquatic varanids. *Varanus mertensi* are a wide ranging, active foraging and opportunistic predator of aquatic areas throughout their northern Australian distribution.

7.3 *Varanus mertensi* found in the ORIS

7.3.1 *Varanus mertensi* found in the ORIS and EK/VRD bioregion

The plasticity of *V. mertensi* to either move between waterbodies or burrow and become inactive shows the species can avoid remaining active in unfavourable areas of the ORIS. This should be considered in future studies of the use of waterbodies by *V. mertensi* both within the ORIS and across its northern Australian distribution. Long-term movement data showed some individuals remain in waterbodies of the ORIS year round. Others extensively utilised these waterbodies but did not remain exclusively within them. The mobility of *V. mertensi* was illustrated by the movements of several individuals between the Packsaddle Main Irrigation Channel and Lake Kununurra Foreshore. These individuals moved a

minimum of 1-2 km's between their core activity areas in each of these waterbodies. Alternatively, inactivity by *V. mertensi* does not require individuals to move from an unfavourable area. Rather individuals simply burrow and become inactive awaiting more favourable conditions. Dry season inactivity should also be considered in future studies of the use of waterbodies by *V. mertensi*.

Varanus mertensi foraged in many different waterbodies of the ORIS including; irrigation channels, farm dams, swamps and Lake Kununurra. However, individuals were rarely observed foraging in irrigation waterbodies, such as gated farm lot supply channels, which remain predominately dry and are only rarely filled with water. This suggests the presence of water alone does not indicate a suitable foraging area for *V. mertensi*. In contrast, a more constant supply of water in channels such as the IPM1 and the PSMIC supports numerous foraging *V. mertensi*.

This study showed *V. mertensi* successfully utilise many human-altered waterbodies of the ORIS. The suitability of some irrigation waterbodies to activity by *V. mertensi* was illustrated by the repeated sighting of over 1 individual km^{-1} along a length of IPM1. Waterbodies of the ORIS are different to most natural waterbodies inhabited by *V. mertensi* in the East Kimberley/Victoria River Downs Bioregion and throughout the wider northern Australian distribution. Most irrigation channels have a near constant year round water supply along their entire length. Conversely, most natural watercourses of the region dry to sporadic pools during most of the year and only experience brief periods of flow during the wet season. *Varanus mertensi* have adapted to utilise the entire length of constantly flowing irrigation channels like IPM1 as indicated by sightings of more than 1 individual km^{-1}. In contrast, *V. mertensi* inhabiting natural watercourses are only able to utilise small sporadic pools along their length during extended dry periods. This restricts the numbers of individuals along such watercourses to the carrying capacity of these pools. The restricted long-term movements of several different individuals within single waterholes along natural watercourses such as Alligator Creek, Four Mile Creek and Salerno Gorge illustrated this. Larger numbers of individual's km^{-1} may result from the utilisation of entire irrigation channels within the ORIS compared to similar lengths of natural seasonal watercourses throughout the East Kimberley/Victoria River Downs Bioregion.

7.3.2 Summary

This field study of *V. mertensi* in the ORIS shows many waterbodies within the scheme are utilised by *V. mertensi*. The damming of the Ord River and construction of the ORIS has resulted in a near constant water supply within many waterbodies of the scheme which are now used extensively by the semi-aquatic *V. mertensi*. Utilisation of these waterbodies, while retaining the flexibility to avoid activity in unfavourable areas, suggests *V. mertensi* are not solely reliant on these waterbodies. *Varanus mertensi* should thus be considered an "opportunistic user" of human-altered waterbodies within ORIS. Although construction of the ORIS has provided many aquatic habitats which are utilised by *V. mertensi* these same aquatic habitats may also provide ideal habitat for cane toads upon their immanent arrival in the Kimberley region. This may represent a significant drawback to the construction of the ORIS in providing suitable aquatic habitats for exotic introduced species such as *Bufo marinus*.

7.4 Scope for future studies

7.4.1 *Varanus mertensi*

This study significantly expanded our understanding of the ecology and behaviour of *V. mertensi* allowing comparison between *V. mertensi* and other varanids. Despite this, considerable scope remains for developing our understanding in both these areas.

Although reporting on the reproductive seasonality of both sexes, time of hatchling emergence, mating season and egg deposition period, this study did not determine the nest sites used by female *V. mertensi*. Not only would this broaden our understanding of *V. mertensi* but expand our limited understanding of the use of nests and nest site selection by varanids. Despite regularly locating over 30 radio-tagged adults, no female *V. mertensi* was observed depositing her eggs during the field study. Future studies examining the nests of *V. mertensi* may adopt a similar methodology but may also benefit from more intense observations of known gravid radio-tagged females during the egg deposition period of December – June.

Despite collecting over two years of data on the long-term movements of numerous radio-tagged adult *V. mertensi* this study was unable to determine if individuals use a defined home range during their lifetime. To successfully do this

would significantly expand our understanding of the long-term movements of wide ranging varanids. To be confident in reporting on the home range of *V. mertensi* a detailed study of the movements of radio-tagged individuals spanning the lifetime of those individuals would be required.

To further expand our understanding of *V. mertensi* and varanids in general, future studies could aim to expand on the four aspects of the ecology and behaviour of *V. mertensi* examined in this study. Specifically future studies could examine *V. mertensi* found in natural waterbodies across their northern Australian distribution. This may provide an appreciation of the similarities and differences between the ecology and behaviour of *V. mertensi* and other varanids within their respective natural environments. However, this should not detract from the findings of this study of *V. mertensi* found predominantly in human-altered waterbodies of the ORIS as this study provided great insight into *V. mertensi*, varanids in general and the use of the ORIS by *V. mertensi*.

7.4.2 Fauna in the Ord River Irrigation Area

This study of *V. mertensi* in the ORIS provided insight into the use of waterbodies within the scheme by a semi-aquatic varanid lizard. If future studies of other fauna found in these waterbodies prove as informative, then we would considerably advance our understanding of how fauna utilise waterbodies of the ORIS. Such an understanding is required to make informed future water management decisions towards conserving biodiversity within waterbodies of the internationally significant Ord River. To achieve this level of understanding, considerable scope remains for both further studies of *V. mertensi* and other fauna found in waterbodies of the ORIS.

To further understand the use of waterbodies within the ORIS by *V. mertensi* knowledge of the recruitment of successive generations within the scheme is required. This would further our understanding of any possible benefits to *V. mertensi* utilising the many watercourses of the ORIS. Recruitment could be examined in a long-term capture-mark-recapture program initially targeting the capture of hatchlings during the months of December – January. The successful recruitment of these hatchlings through to adulthood could then be followed through further captures in subsequent years.

To develop our understanding of how different fauna utilise waterbodies of the ORIS we must first know what species use these areas and at what times during the year. This could be established through compilation of an ongoing season–to-season faunal inventory for waterbodies of the ORIS which identifies both endemic and migratory fauna. With this information further studies of other fauna could be initiated and successfully undertaken. Such studies could include an examination of the use of waterbodies within the ORIS by migratory fauna such as waterbirds. This would provide valuable contrasting insight to that on the extensive year-round use of waterbodies of the ORIS by *V. mertensi*. In undertaking this, a seasonal inventory of waterbird species found in waterbodies of the ORIS would prove invaluable.

Given the current debate over future management strategies for the ORIS it is paramount that further studies begin to examine how fauna utilise the many waterbodies of the ORIS. Such studies may benefit from adopting a similar style to this study given the insights provided on the use of waterbodies within the ORIS by *V. mertensi*. If this is undertaken then future management strategies could be adopted that consider fauna found in the ORIS.

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